zoosystema

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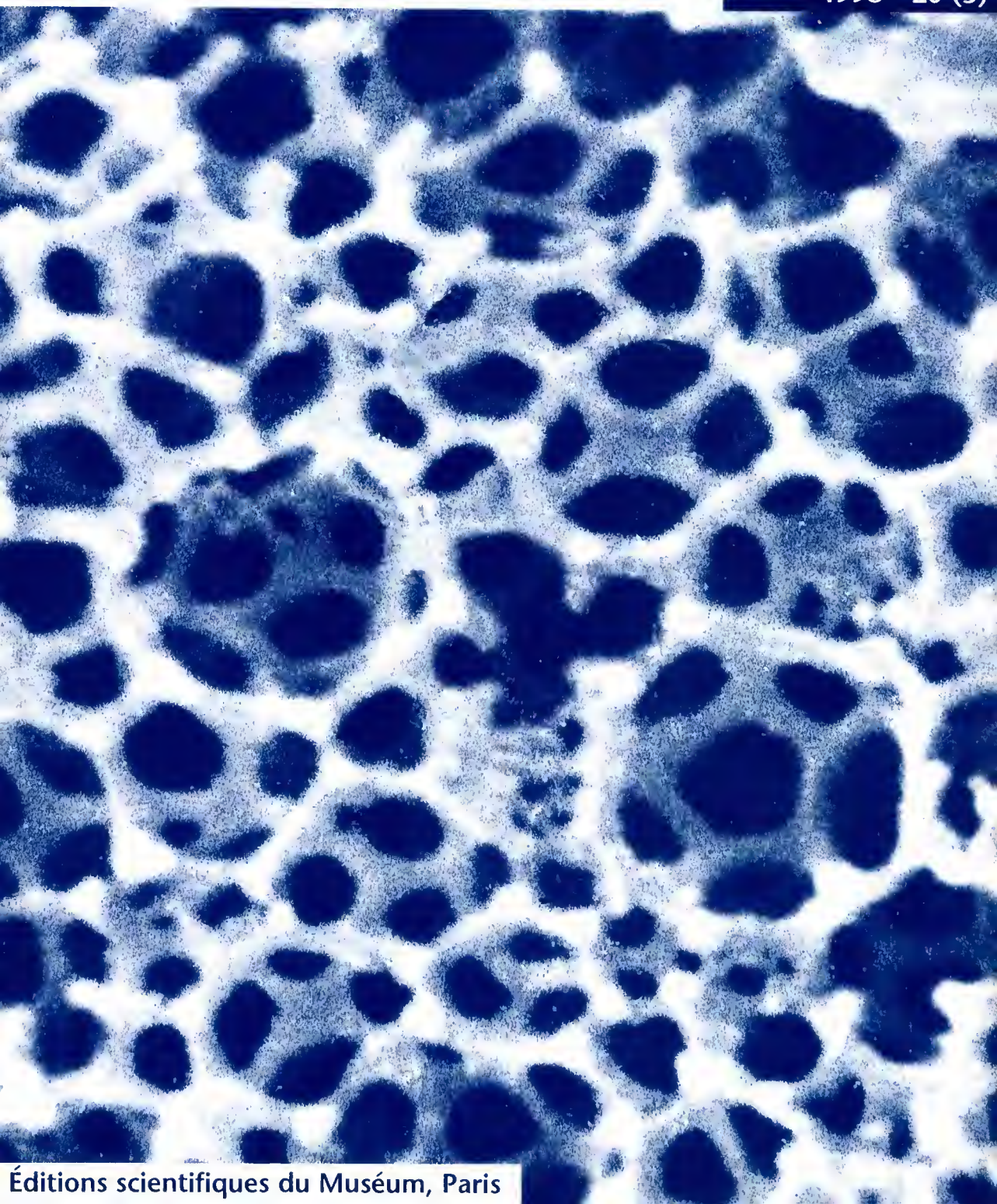

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An enigmatic filiform organism in the epicardium cavity of a new polycitorid ascidian

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ABSTRACT
In several samples of the ascidian *Eudistoma hospitale* n.sp. collected in the western Pacific Ocean and in South Africa, a filiform organism was found implanted on the heart tissue. It is rolled in balls, occupies a large parr of the ascidian abdominal cavity, and reaches such a length that it bursts through the branchial sac and finally comes out at the colony surface with a free tip. Present in all zooids and in larvae, always single, this filament remains of an unknown nature, despire all cytochemical and microanalytical methods used ro characterize it. This kind of organism has never been recorded in any other ascidian.

KEY WORDS
ascidians,
systematics,
parasitology.

RÉSUMÉ
Un énigmatique organisme filiforme de la cavité épicardiale d'une nouvelle espèce d'ascidie polycitoride. Dans tous les spécimens de l'ascidie *Eudistoma hospitale* n.sp. récoltés dans le Pacifique occidental et en Afrique du Sud, un organisme filiforme esr implanté dans les tissus du cœur. Le filament est roulé en pelote et occupe la plus grande parrie de la cavité abdominale de son hôte. Il arreinr une longueur telle qu'il est expulsé dans la caviré branchiale et que, finalement, son extrémité libre sort de la colonie. Présent dans tous les zoïdes et les larves, le filament resre d'une nature inconnue malgré les méthodes de cytologie et de microanalyse utilisées pour le caractériser. Ce type d'organisme n'avait jamais été rencontré dans une ascidie.

MOTS CLÉS
ascidies,
systématique,
parasitologie.

INTRODUCTION

An encrusting colonial ascidian shows curious thin threads located inside the zooids (Fig. 1E) and sometimes coming out to the surface through the oral apertures. This species was collected for the first time at the Chesterfield Islands (southwest Pacific) in July 1988, and later in Septembet 1996; it was also collected on Fiji in 1991 and October 1996, and in February 1994 and 1996, it was found in two widely separated stations in South Africa.

MATERIAL

Chesterfield Islands (Laboute coll.). Skeleton, 30 m; Île Longue, 22 m.
Fiji Islands. Nukubalavu, 10 m, 16°45'06S - 179°47'83W (Coral Reef Reseach Foundation coll).
South Africa. Sodwana Bay, 19 m (Schleyer coll.); South Cape coast, intertidal (Glassom coll.).

METHODS

Specimens fixed in 4% formaldehyde in sea water were dissected, stained and mounted on slides for general anatomical observations. Sections of 7 µm were stained with hemalum-picroindigocarmine or toluidine blue to reveal the morphology of the tissues. Ultrathin sections were observed with an Hitachi 600 electron microscope. Dissected filaments were critical-point dried, coated with gold and examined with a Jeol JSM 840 microscope.
Several cytochemical reactions were used (Pearse 1968; Gabe 1968; Ganter & Jolles 1968-1970). They are:
– the periodic acid Schiff reaction (PAS) for glucids and glycoproteins;
– the Lugol's iodine reactive for glycogen;
– alcian blue at PH 0.5 and 2.5 for acidic glucids
– the alloxane-Schiff reaction for proteins;
– the ferric ferricyanide method (Schmorl's and Lillie processes) for thiols and other reducing groups especially purines and sulphides;
– the Masson's argentaffin reaction for phenols (tunichrome and analogues);
– the coupled tetrazonium reaction of Danielli, using the fast blue B salt for proteins and phenols;
– the 1-(4-chloromercuriphenyldiazo)-2-naphtol (mercury orange, red sulphydril reagent) and the 2.2'-dihydroxy-6.6'dinaphtyl disulphide (DDD) methods for thiol groups;
– the Lugol's sulfuric acid for cellulose;
– the chlor-zinc-iodine for both chitin and cellulose;
– the ferric chlorure-acetic acid for porphyrins.
Elementary microanalysis was performed on paraffin sections spread on carbon-coated mylar slides, using a CAMECA MS46 electron microprobe equipped with wavelength dispersing spectrometers. The diameter of the probe was 1 µm. Molecular analysis was carried out on similar sections using a Raman laser microprobe Dilor Microdil 28.

RESULTS

THE ASCIDIAN

Family POLYCITORIDAE Michaelsen, 1904
Genus *Eudistoma* Caullery, 1909

Eudistoma hospitale n.sp.

TYPE MATERIAL. — MNHN A3 Eud 188, Chesterfield Islands.

DESCRIPTION

All samples have the same colonial structure: cushions or crusts reaching several decimeters across and up to three centimeters thick. The colour in life is uniform through each colony, but in only one station varies among black, light brown, pink or purple (Fig. 1A-D). The colony surface is smooth, shiny, sometimes slightly undulated. The zooid oral openings appear as small holes arranged in circles in the center of which the cloacal apertures open, grouped on small protrusions (Fig. 1A-D). The tunic is opaque without any embedded sediment. The general consistency is firm with an even more resistant surface layer. When fixed, the tunic becomes more translucent and more or less dark grey. It contains abundant vesicular and pigment cells, and vanadocytes. The zooids lie perpendicular to the colony surface; the less contracted

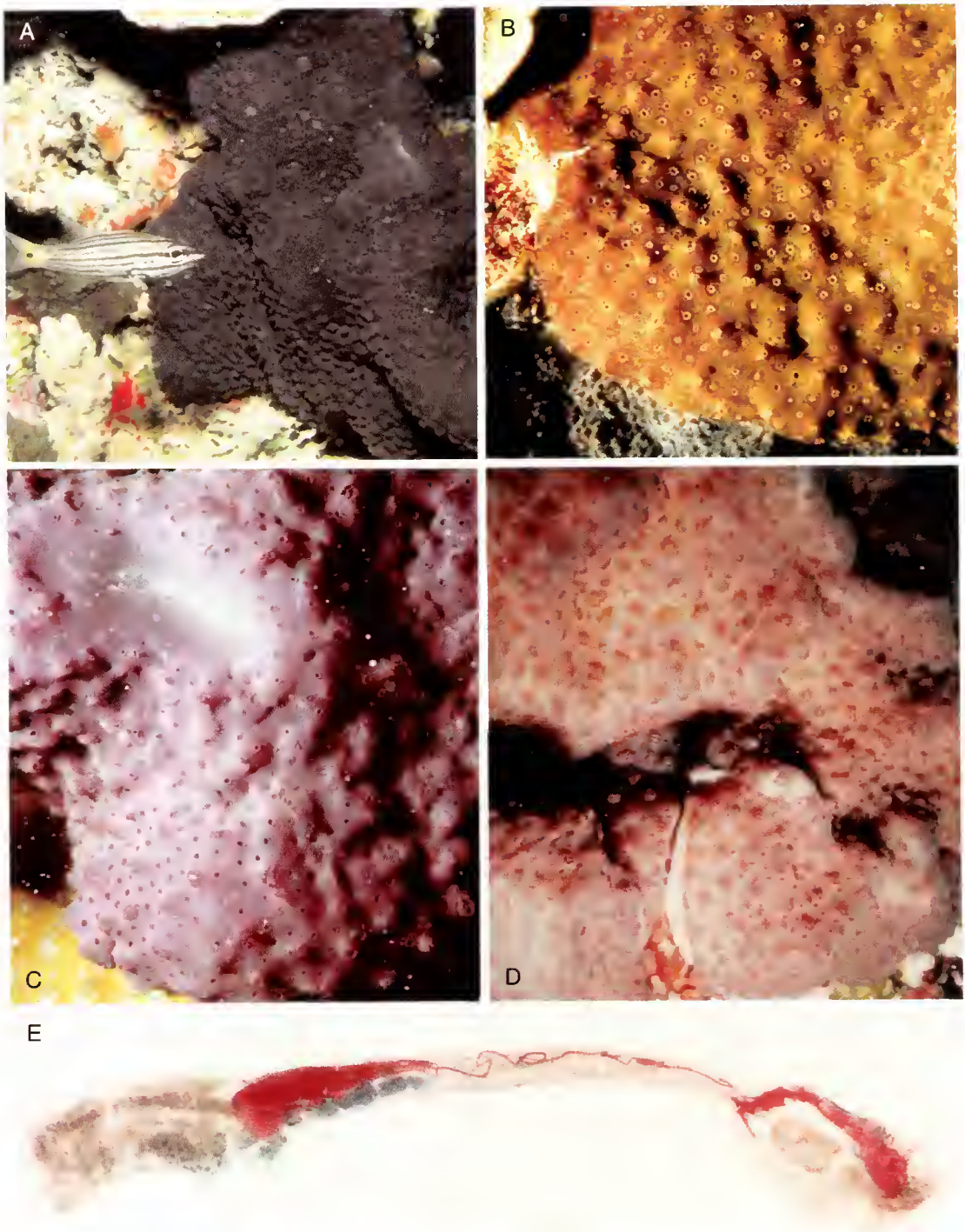

FIG. 1. — *Eudistoma hospitale* n.sp.; **A**, **B**, **C**, three different colours of colonies from the Chesterfield Islands, **D**, colony from Sodwana Bay, South Africa; **E**, a zooid, 1 cm long, with its thread stained in red with acidic fuschin.

ones easily reach 1 cm in length. The thoracic body wall is black, especially in the anterior part. The abdomens are yellowish, the embryos bright orange, the larvae paler orange. These colours disappear after fixation.

The zooids all have the same characters, whatever their geographical origin. Both siphons are tubular, edged with six rounded lobes, the cloacal siphon longer (Fig. 2A, C). The endostyle is thick. The thoracic muscles are dense with numerous longitudinal and transverse fibers. Generally, sixteen oral tentacles in two orders of size alternate along two circles. The branchial sac has anteriorly an imperforated area only seen in relaxed zooids. An average of twenty-five elongated stigmata were counted in the first row.

The abdomen lies below a constriction of the body. The isodiametric œsophagus is very long (Fig. 2A). The stomach has a generally round shape with sometimes, in the largest individuals, two lateral crests when the gut is empty. The post stomach is cylindrical, separated from the mid-intestine by a constriction. The rectum begins with an annular widening (Fig. 2E, F) which sometimes forms two crescent-shaped caeca. After the curve of the gut loop, the intestine remains parallel to the œsophagus up to the level of the second stigmata row, where the rectum opens via a bilobed anus. Beyond the mid-intestine the rectum has a green colour in life. At the stomach level, the rectum is covered with parallel pyloric tubules converging into a short duct that connects with the posterior part of the stomach. One or two vascular processes prolong the abdomen into the tunic.

The heart forms a J-shaped tube, with unequal sides, more or less inflated (Fig. 2D-F). The endothelium of the vessels disappears at a short distance from the heart. On the cardiac tissue, between the ovary and the base of the gut loop, there is an extremely long filiform structure, of unknown nature. This thread begins with a conical root (Figs 2D, E, 3C, D, 4A), then remains the same diameter along its whole length. It is coiled on itself (Figs 2D-F, 4A), and invades the epicardium cavity (Fig. 1E). Reaching the thorax, it becomes so voluminous and tightly wound that it pierces the wall, enters the branchial sac and finally extends out through the oral siphon.

The gonads have the common structure of the genus. The testis is made of numerous round vesicles (Fig. 2A, B); the ovary is located in the center of the gut loop, below the stomach (Fig. 2F). In colonies from the Chesterfield Islands, the zooids are all male or female; but in ones from Fiji there is a young ovary amidst the testis vesicles and embryos are present in the cloacal cavity (Fig. 2C). The South African colonies are simultaneously hermaphroditic.

One or sometimes two embryos are incubated at the same time. Well-developed larvae were found only in Chesterfield specimens (Fig. 2G, H). They remain inside the tip of the oviduct until their release into the sea. The larval trunk is oval, 1 mm long. The tail makes a half turn around it. When younger embryos are orange and translucent, the tadpole body wall contains numerous pale opaque cells. The sensory vesicle has the usual otolith and ocellus. Three rows of about fifteen stigmata apiece are already visible in an incubating larva (Fig. 2H), and an embryonic gut lies in the posterior part of the body (Fig. 2H). Anteriorly, the three adhesive papillae, all in a line, have oval tips. Their thick bases alternate with four foliose vesicles. In addition, there is a vesicle applied on the side of the most dorsal vesicle on each side (Fig. 2H). In aged larvae, a short thread can be seen in transparency amidst the vitellus near the embryonic gut (Fig. 2G). The presence of this filamentous structure has been ascertained in histological sections.

Within the tunic, between functional zooids, traces of degenerated zooids persist with pieces of filaments which are only empty tubes, some with lysed cells. No filaments were found in the tunic outside the zooids.

Eudistoma hospitale differs from other species of the genus only by its larval structure and the constant presence in all colonies and all zooids of a filiform organism whence the species name.

The filamentous structure

A single thread winds about inside the pericardial cavity of each zooid (Figs 1E, 4C). Its conical basis takes root on the cardiac lining of the ascidian and is externally covered by a cellular layer of the same constitution as the heart's endothelium (Fig. 3C, D). An aperture allowing a com-

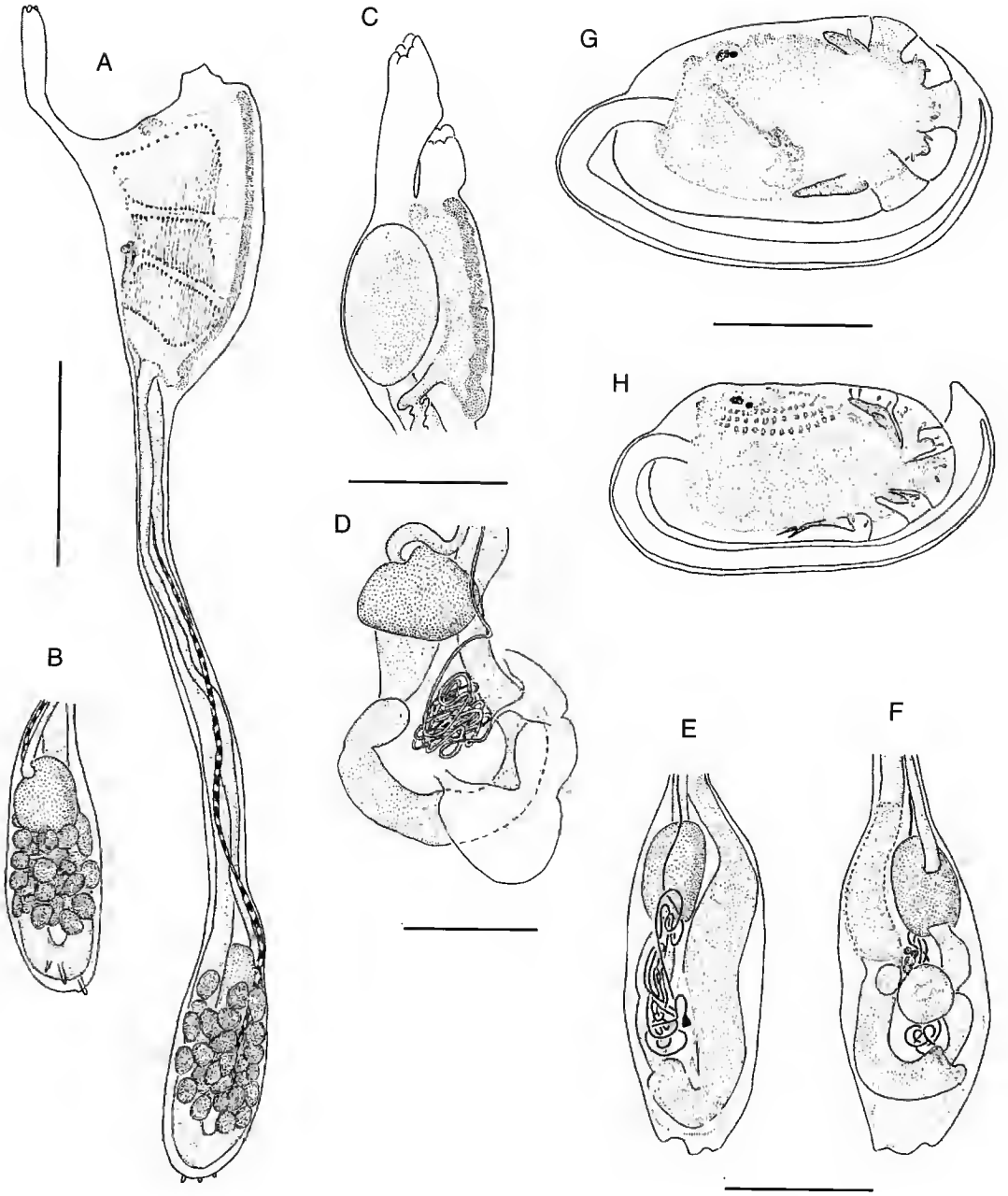

FIG. 2. — *Eudistoma hospitale* n.sp.; **A**, right side of a relaxed zooid with male gonad (thread not figured); **B**, left side of the gut loop of the same zooid; **C**, thorax with an incubating embryo; **D**, posterior part of an abdomen dissected to show an hypertrophied heart and its filament on the digestive loop; **E**, **F**, both sides of the gut loop of a zooid with ovary; **G**, larva with a filament seen in transparency; **H**, aged larva with well-developed branchial sac and gut. Scales bars: A, B, 2 mm; C, E, F, 1 mm; D, G, H, 0.5 mm.

munication between the cardiac cavity and the inside of the filament is clearly visible in scanning electron microscopy after dissection and critical point dehydration. Following the basal part which measures approximately 100 µm in diameter, the thread rapidly narrows, and then remains of a constant diameter of 20 µm along its whole length (Figs 3A, 4A, C). At first only slightly coiled, the thread lengthens during the zooid's growth, and becomes a more and more tightly coiled ball (Figs 1E, 2D, E, 4C) that invades the whole abdomen and teaches the thorax. There the filamentous structure is so large that it breaks the thorax floor, spreads freely into the branchial sac, and finally comes out through the oral siphon. On the colony surface, we have found unrolled flexible threads reaching 1 cm in length. The length of the thread of an uncoiled ball measures about 10 cm.

The structure of the thread comprises three parts.

The external sheath of parietal cells

The external sheath of the filament seems to be made of cells originating in the cardiac endothelium of the ascidian with which it is in continuity at the level of its conical root (Figs 3C, D, 4A). There, the cells are thick, spherical, covered with villosities, with a spherical nucleus. These cells progressively flatten along the internal filament the farther they lie from the heart (Fig. 3C, D). Their nucleus become kidney-shaped (Fig. 4D, E), long villosities persist (Fig. 4B, D); and the basal layer is thin. In light microscopy, the nucleus is strongly stained, and the reduced cytoplasm is constituted almost entirely of microvillosities. In electron microscopy, we established that a clear limit exists between this cellular envelope and the filament lining itself, without interpenetrations (Fig. 4E). As the thread lengthens, its external cells become progressively very much flatter and less tightly packed and seem to be only linked by their villosities, which cover the whole filament.

The filament lining

The filament has a thick wall which is not segmented and neither interiorly nor exteriorly ornamented. The external surface is totally smooth when observed in SEM or TEM (Figs 3B, 4D-F). The internal surface is granular, in close contact with the cells inside which seems responsible for its secretion. No stratified structure is revealed by TEM in this 2 µm thick wall (Fig. 4F). The tube is devoid of cellulose: the Lugol-sulfuric acid mixing reaction is negative, while on the contrary, it is positive for the ascidian host-tunic. The presence of chitin seems ruled out for the reaction with chlor-zinc-iodine (also revealing cellulose) is negative. A microanalysis in Raman spectroscopy presents a single peak centered on 1450 cm^{-1}, then the absence of chitin. The hypothesis that the filament is a fungus closely allied to the *Trichomycetes* is excluded by these result.

The internal cells of the filament

The cells of the filament have two different aspects (Fig. 4D); they may belong to two different kinds of cells or represent two states of evolution of a same kind of cell, as the ratio of the chromophile cells increases in the distal part of the filament. However, no transition state was observed between these two cellular aspects. In both cases, the cells have a round outline and a large central nucleus (Fig. 4D, E), thus belonging to an eucaryote. The cells are pressed against each other in the whole length of the filament. They seem to be bound together and to the wall by a substance containing microgranules. Histological stains (Masson's trichrome, toluidine blue) show a difference between two cellular aspects (Fig. 4B): cells with a clear homogeneous cytoplasm with a central nucleus rich in chromatin, and chromophile cells, slightly larger, whose cytoplasm contains multiple vacuoles with a dense content (Fig. 4D, E).

The vacuoles' contents have two peculiar characters: a strong reactivity to the Lugol treatment and the coexistence of sulphur and vanadium as revealed by X-ray microanalysis. The coloration obtained with Lugol's reagent is intense and immediate; it produces a brown-red tint. So it differs from the purple color of animal and vegetal glucids, which, anteriorly the chemically based techniques, were considered as specific of these compounds. Such anomalies in the results of the reaction were recorded in the search for

glucids in sporozoans and had led to the notion of "paraglycogen" Grassé (1953). The absence of reactivity to PAS as Pearse (1968) noted in criticism of this old technique (proteins being able to positively react as well), let us conclude that the vacuole content is not glucidic nor glycoproteic.

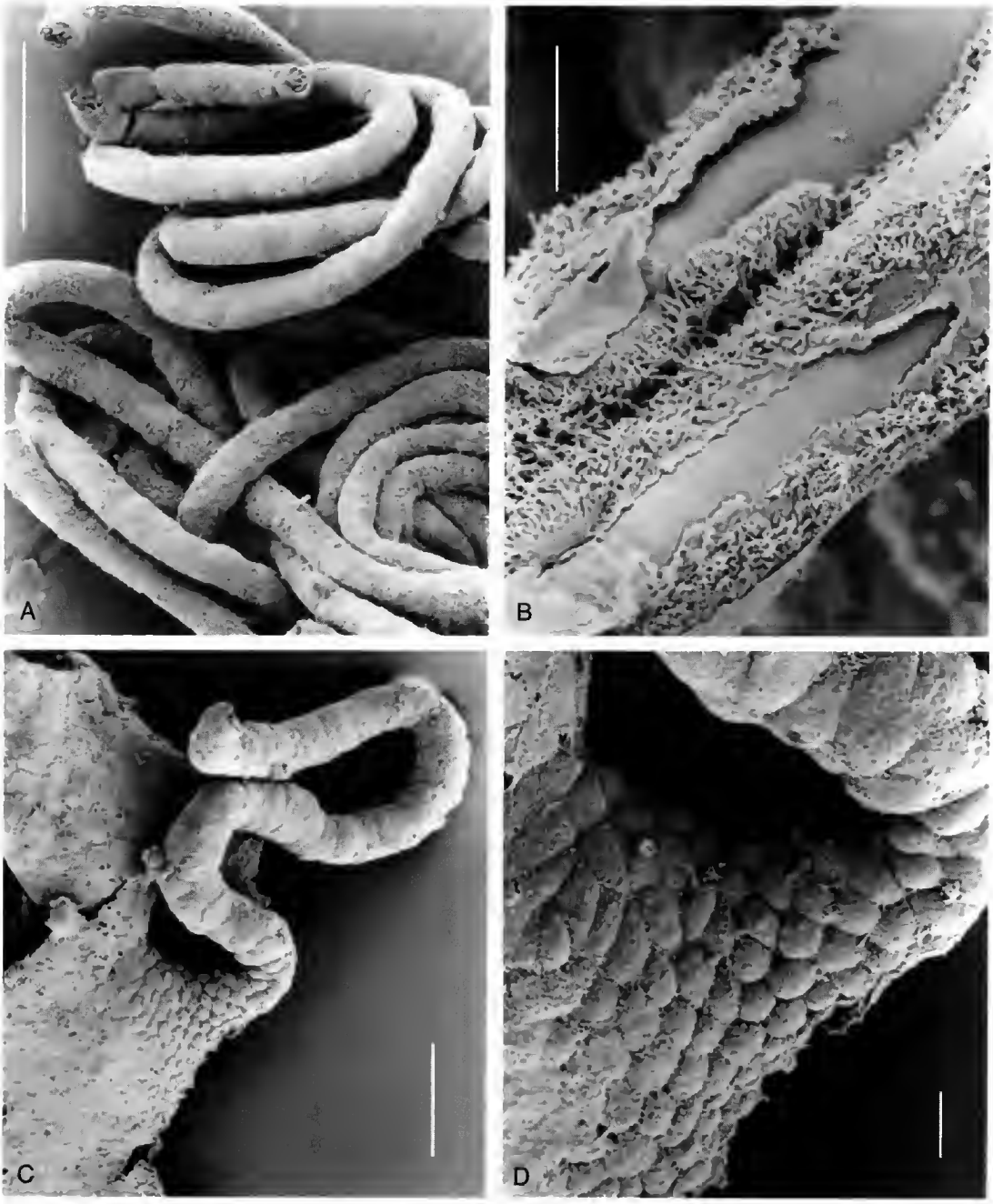

FIG. 3. — **A**, part of a thread ball; **B**, parietal sheath disrupted, showing the filament; **C**, thread root inserted on the heart tissue; **D**, detail of the root showing the progressive flattening of the parietal cells. Scale bars: A, 100 µm; B, D, 10 µm; C, 50 µm.

The coexistence of sulphur and vanadium has often been demonstrated in ascidian vanadocytes. We have previously shown (Martoja *et al.* 1994) that only a part of the sulphur is linked to the vanadium; this occurs in only two kinds of cells, compartment cells and signet ring cells, while in morula cells the vanadium is linked to oxygen and coexists with a tunichrome. The elimination of vanadium by normal hydrochloric acid or Schmorl's reagent, though maintaining the sulphur, does not unmask thiol groups (negatives reactions with ferric ferricyanure or red-sulfhydril reagent). So it is not possible to equate the vacuole content of the filament cells with that of the vacuoles of the signet ring cells and compartment cells. Masson's argentaffin reaction being also negative, the presence of a tunichrome is also excluded, which rules out a similarity with the host's morula cells. The vanadium ligand seems very different from that of the host. The hypothesis of a porphyrin-vanadium compound is also excluded because protracted treatment with chloroform (24 h), the best solvent of porphyrins, has no effect on the composition of the vacuolar content, and the ferric chlorure-acetic acid reaction is negative. The problem of the vanadium ligand remains unsolved.

The samples were fixed in the field with seawater-formalin, which does not allow for a more precise or advanced histological examination than what we have done.

DISCUSSION

It is difficult to determine whether this curious filament represents a parasite or a symbiont. At first, the hypothesis of a peculiar organ, excretory for example, in a particular ascidian species was considered but rapidly abandoned: the filament develops in a natural cavity without any link with its wall, then bursts through the branchial sac and even extends a lengthy free extremity outside the ascidian. The cells of the filament have not the usual characters of excretory cells. The coating of ascidian cells along the thread more likely suggests a host's reaction against a foreign organism, analogous to the cysts that ascidians make around endovascular parasitic copepods (Dudley 1968). The absence of any differentiated tissues that compose the filament excludes the possibility of a parasitic copepod, even a very modified one. Assignment to a particular metazoan phylum remains unsettled. The large central nucleus and the thin cell membrane exclude, as well, bacteria, procyanophytes and algae. No known fungi correspond to this structure, nor does the chemical composition of the filament support such an affiliation.

Influence of the filament on its host

The zooids of *Eudistoma hospitale* do not show any peculiarity which may be due to the influence of the filament, for example no morphological deformation, no castration. The zooids feed normally, their gonads are well-developed, their embryos reach full maturation without monstrosities. Asexual reproduction is not affected either, as the colonies teach very large sizes compared to other species of the same genus.

Transmission mode

We do not know if the organism which forms the filament goes through its life cycle a free living stage or obligatorily housed at all times in a host. We only notice that the association begins from the larval stage of the ascidian, as a short filament is already present in the larva that is being incubated in the oviduct, before its release into the sea. "Infection" thus may take place in the mother zooid before the young tadpole begins to elaborate its tunic, perhaps at the level of the cells of the egg envelope. This would imply that, in addition to embedded cells inside a filament, isolated cells or gametes would exist and circulate with the host's blood, equally able to infect eggs and the regenerating buds produced by strobilation responsible for the asexual growth of the colony. Another hypothesis would take into account the emission of the filament extremity at the colony surface, allowing cells to be liberated in sea water and ingested to infest newly formed zooids. A direct transmission through the colonial tunic from one zooid to another is also a possibility.

Presently nothing allows us to explain why there is always just a single thread per zooid and we have found no gametes.

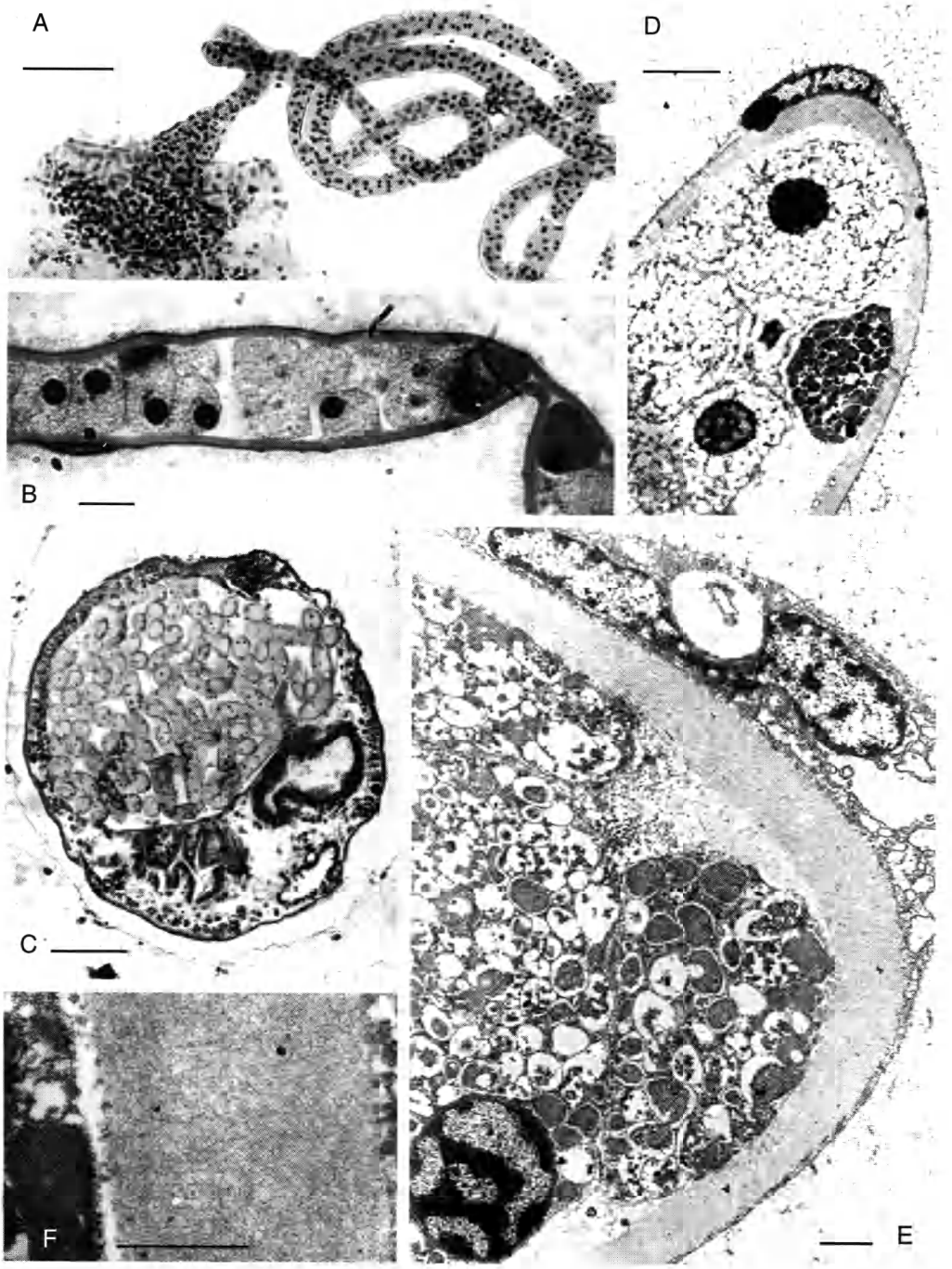

FIG. 4. — **A**, **B**, cardiac extremity of a thread in light microscopy (toluidine blue). **C**, sections of a thread ball contained in the pericardium cavity occupying the most part of the abdominal section of a zooid. **D**, **E**, sections of a thread in TEM showing parietal cells with elongated nucleus and microvillies, the tube wall, the internal granular and vacuolated cells. **F**, detail of the filament wall. Scale bars: A, 50 µm; B, 10 µm; C, 100 µm; D, 5 µm; E, 2 µm; F, 1 µm.

Other commensals, symbionts or parasites known in ascidians

Organisms living in association with ascidians were reviewed by Monniot (1990). They are very numerous: Virales, Bacteria, Flagellata, Trichomonadina, Rhizopoda, Gregarina, Coccidia, Haplosporidia, Ciliophora, Nephromyces, Algae, Cnidaria, Ctenaria, Turbellaria, Annelida, Bryozoa, Nemertina, Mollusca, many Crustacea and especially copepods, and also Pisces.

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I have greatly benefited from the precious knowledge of R. Martoja in cytology, and I thank him as well for the cytochemistry and microanalyses he has performed as for the thoughtful discussions we had during this study. I am much indebted to T. Newberry for the english language corrections.

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Two new species of the genus *Ophiuraster* (Ophiurinae, Ophiuroidea, Echinodermata) from French collections and some remarks on the genus

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Litvinova N. M. 1998 — Two new species of the genus *Ophiuraster* (Ophiurinae, Ophiuroidea, Echinodermata) from French collections and some remarks on the genus. *Zoosystema* 20 (3) : 439-444.

ABSTRACT
Two new species of the poorly known genus *Ophiuraster* (Ophiurinae, Ophiuroidea, Echinodermata), *O. belyaevi* n.sp. from Kerguelen Islands and *O. patersoni* n.sp. from Bay of Biscay are described on the basis of the collection of the Muséum national d'Histoire naturelle, Paris. The genus is characterized by a combination of plesiomorphic and apomorphic features. The distribution of these species is shown on a map.

KEY WORDS
Ophiuroidea, Ophiurinae, *Ophiuraster*, *O. belyaevi* n.sp., *O. patersoni* n.sp., systematics.

RÉSUMÉ
Deux nouvelles espèces du genre Ophiuraster *(Ophiurinae, Ophiuroidea, Echinodermata) de la collection du Muséum national d'Histoire naturelle, Paris et quelques remarques à propos du genre.* Deux espèces nouvelles du genre *Ophiuraster* (Ophiurinae, Ophiuroidea, Echinodermata) sont décrites à partir des collections du Muséum national d'Histoire naturelle, Paris : *O belyaevi* n.sp. des îles Kerguelen et *O. patersoni* n.sp. du golfe de Gascogne. Le genre est caractérisé par la combinaison de caractères plésiomorphes et apomorphes. La carte de la répartition de ce genre, très peu connu, est donnée.

MOTS CLÉS
Ophiuropidea, Ophiurinae, *Ophiuraster*, *O. belyaevi* n.sp., *O. patersoni* n.sp., systématique.

INTRODUCTION

The genus *Ophiuraster* was established by H. L. Clark (1939). It includes very small brittle stars, having disks that are poorly differentiated from the short and wide arms. Large, closely connected plates border the dorsal and ventral margins of the disk. As a result the brittle stars of this genus resemble some sea stars of the Family Goniasteridae. Only two species of this genus have previously been described each represented by only one specimen. I found two undescribed species of this genus in the collection of the Laboratoire de Biologie des Invertébrés marins et Malacologie of the Muséum national d'Histoire naturelle, Paris. The unusual characters of these species broaden our understanding of this genus. The genus *Ophiuraster* includes now four species: *O. perissus* Clark, 1939; *O symmetricus* Fell, 1958; *O. belyaevi* n.sp.; *O. patersoni* n.sp. The map of distribution of the genus is given (Fig. 1).

Order OPHIURIDAE
Suborder CHILOPHIURINA
Family OPHIURIDAE
Subfamily OPHIURINAE

Ophiuraster belyaevi n.sp.
(Fig. 2)

HOLOTYPE. — One specimen, (MNHN EcOs 5839) collected off Kerguelen Islands, *Marion-Dufresne* MD-04 cruise, stn I-106, CP 258, 48°43'5"S - 71°06'5"E, 925 m, 13.III.1975.

ETYMOLOGY. — The species is named to honour my teacher, late Professor Georgy Michailovich Belyaev, a specialist of Echinodermatae.

DIFFERENTIAL DIAGNOSIS. — The new species is distinguished by the absence of dorsal-arm plates and arm spines, vertebrae covered by transparent skin, and a large terminal plate present at the tip of each arm. The new species is more closely related to *O. patersoni* described below than to *O. perissus* and *O. symmetricus.*

DESCRIPTION

The disk diameter is 3 mm, and the arms are short and wide, 2.5 mm in length with a basal width of 1.3 mm. The center of the dorsal surface of the disk is elevated and covered by primary plates: the centrodorsal plate is divided into three small irregularly shaped plates, which are in contact with each other. The radial plates are large, quadrangular and irregularly shaped; one is divided into several pieces by radial fissures. A small interradial plate lies distal to each pair of radial plates. All plates have a porous surface and irregular edges.

The marginal part of the dorsal surface disk is depressed and covered with skin in which the radial shields are embedded. The radial shields are longer than broad and separated by a strip of integument. In each interradius, the edge of the disk is occupied by two quadrangular plates, which meet interradially. The same plates extend to the ventral surface of the disk. They are very large, quadrangular, closely connected and occupy the entire peripheries of the ventral interradius.

The arms appear to be shorter than diameter of the disk. They are wide at their base and connected tightly with the disk. There are no dorsal arm plates. There are six arm joints beyond the edge of the disk, each of which bears protruding lateral arm plates. The lateral plates of each segment are widely separated from each other by a strip of thin integument through which the vertebrae can be seen. The lateral plates of successive segments contact each other. There are no spines in the arms. The end of each arm is occupied by a large widened heart-shaped terminal plate. There are two very small pointed protrusions in the distal end of it that are rather hard to notice. The ventral arm plates are present only in four segments of the arm. The first ventral arm plate is large and rounded. Three distal ones are minute and deeply depressed. The ventral arm plates are widely separated from each other. The second oral tentacle pore opens outside the mouth, and tentacle pores are present throughout the length of the arm. They are small and covered with thin skin that has a central hole for the tentacles. There are neither tentacle scales nor oral shields. The distal part of adoral shield of one of interradius is elevated and bears a large water-pore. The adoral shields are large and irregularly quadrangular. The oral plates are large and have one to three ill-defined oral papillae, of which the apical

papillae are larger. In the depth of the mouth a tooth-like apical papilla can be seen. There is a minute bursal slit in one of interradius.

Ophiuraster patersoni n.sp.
(Fig. 3)

HOLOTYPE. — One specimen (MNHN EcOs4895) collected in Bay of Biscay, *Jean Charcot* BIOGAS VI, Stn 6, DS86, 44°05'N - 04°19'W, 1950 m.

ETYMOLOGY. — The species is named to honour Dr Gordon Paterson who originally identified this specimen up to genus.

DIFFERENTIAL DIAGNOSIS. — The new species closely resembles *O. belyaevi* n.sp., differing from it by the absence radial shields and adoral plates, by the small terminal plate, and in the presence of only primary plates on the disk. It is possible that the only specimen available is not adult and additional material could make the diagnosis more precise.

DESCRIPTION

Disk is flat, diameter 1.9 mm. Arms and disk are not well-differentiated and the animal at first sight resembles a sea-star. The dorsal surface of the disk is covered with transparent skin and large, centrally situated, primary plates with a porous appearance. The centrodorsal plate is divided transversely in two unequal parts. The five radial plates are larger and irregularly rounded. There are no radial shields and the lateral plates of the first segments of arms take their place. Two large, closely connected marginal plates make contact interradially and extend to the ventral side of the disk.

The arms are short and consist of five segments. The arm length is 1.4 mm; the basal width 0.6 mm. There are no dorsal plates in the arms but only large and swollen lateral ones. The lateral plates of each segment are separated on dorsal side of arm by a strip of transparent integument through which the vertebrae are seen. The first pair of lateral plates is small and situated within a range of the disk close to its marginal plates. They could be easily mistaken for radial shields but there are the vertebrae, which can be seen through the skin. The distal lateral plates are larger and more swollen, meeting broadly above and below the arm.

The terminal plates are large; each bears two to

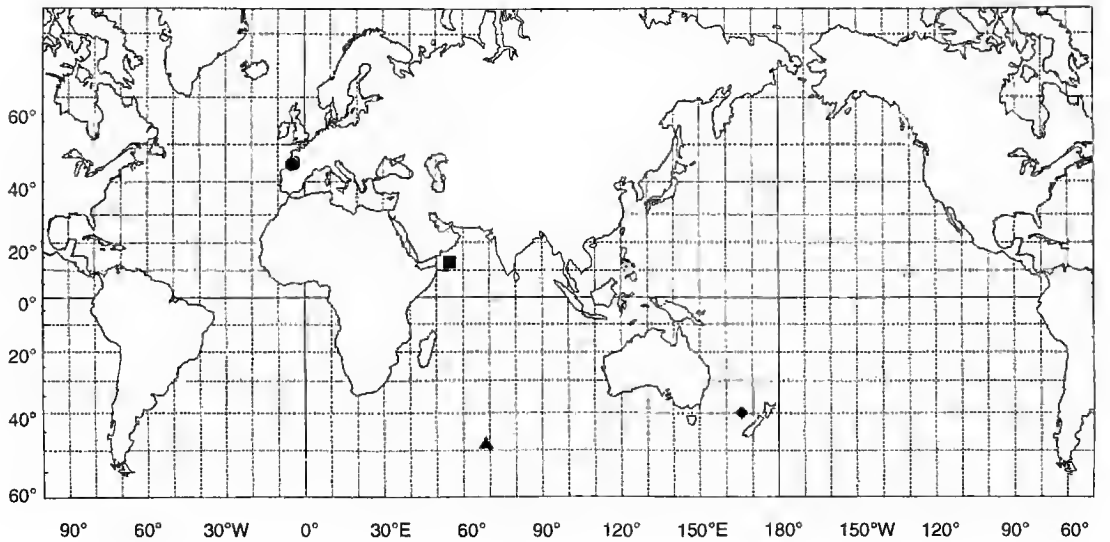

FIG. 1 — Distribution of the species of the genus *Ophiuraster*; ■, *O. perissus* (2312 m); ◆, *O. symmetricus* (720 m); ▲, *O. belyaevi* (925 m); ●, *O. patersoni* (1950 m).

four very small pointed protrusions in the distal end. There are no arm spines. The first ventral plate is large and rounded, the two distal ones are very small and deeply depressed. There are no oral shields or adoral shields. In the place of the oral plates, there are diamond-shaped patches of thin integument.

The long oral plates have small and ill-defined oral papillae. The apical papillae are largest and similar to the teeth situated above them. The second oral tentacle pore opens outside the mouth. The small tentacle pores are present on the full length of the arm. There are no tentacle scales. The ventral interradial side of the disk is

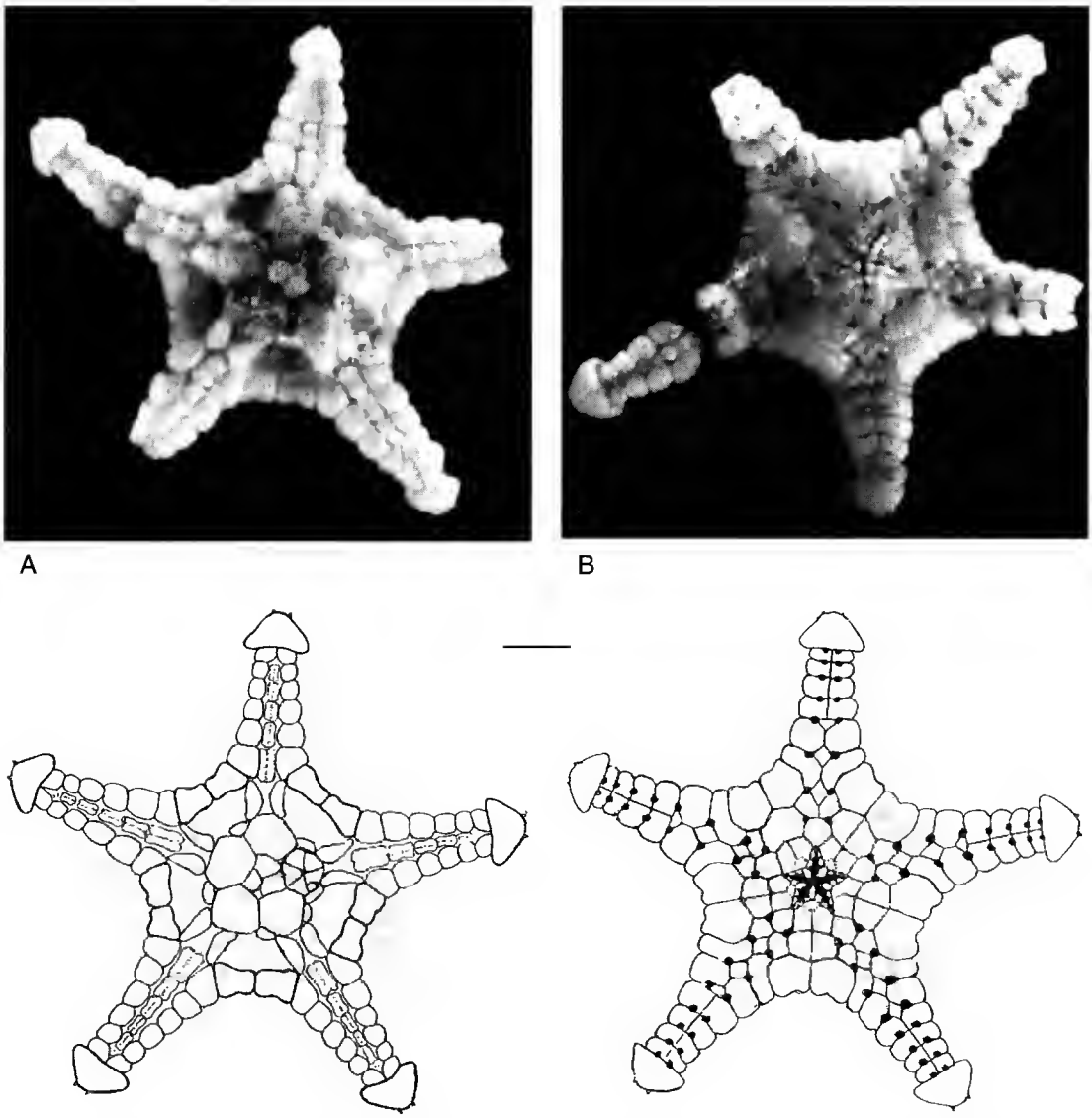

FIG. 2. — *Ophiuraster belyaevi* n.sp., disk diameter: 3 mm; **A**, dorsal surface of disk; **B**, ventral surface of disk. Scale bar: 1.0 mm.

occupied by two large marginal plates, which meet interradially. No genital plates and bursal slits were evident.

REMARKS

A well-preserved crustacea, occupying the whole stomach, is seen through the semi-open mouth. But, because there only was one specimen of this species, it was not possible to extract and identify this animal.

DISCUSSION

There are some contradictions in the interpretation by different authors of some morphological

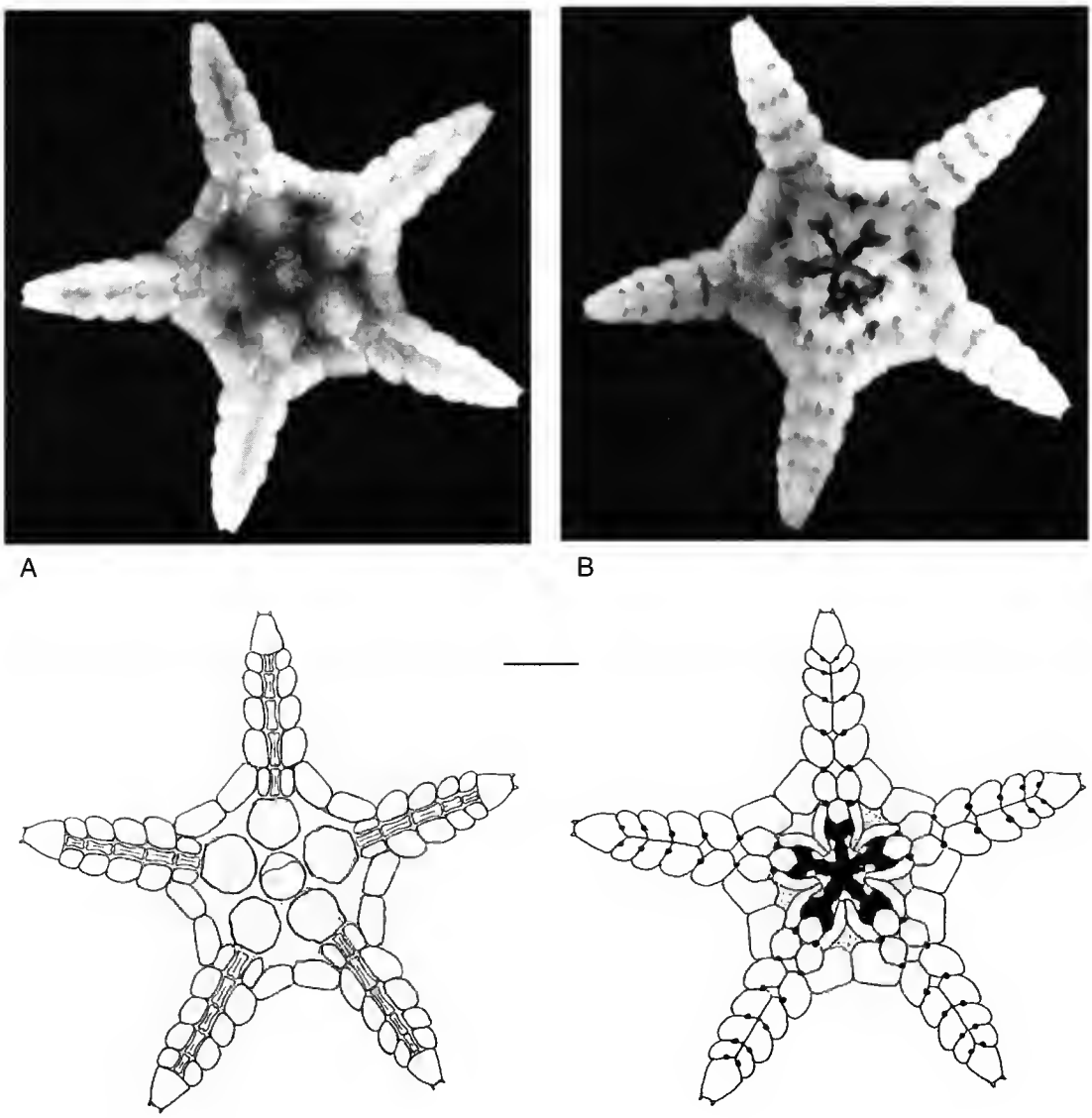

FIG. 3. — *Ophiuraster patersoni* n.sp., disk diameter: 1.9 mm; **A**, dorsal surface of disk; **B**, ventral surface of disk. Scale bar: 1.0 mm.

features of species of this genus. In *O. perissus*, Clark (1939) considered the large marginal plates occupying the whole margin of the disk to be radial shields. Fell (1958) supposed that these plates in *O. symmetricus* were the broadened lateral arm plates. On the basis of these two new species both described from only one specimen, I propose that the plates occupying dorsal and ventral interradial surface are considered as marginal interradial plates of the disk.

H. L. Clark (1939) had noticed that the genus *Ophiuraster* is probably closely related to the genus *Ophiomastus*; Matsumoto (1917) and Vadon (1991) considered that genera similar to *Ophiomastus* are paedomorphic. The species of the genus display a combination, of both paedomorphic and specialized characters. On the one hand the new species have some characters that are typical for juvenile ophiuroids: (1) the arms are extremely short and consist of few segments; (2) the arm spines are absent; (3) the oral shields and adoral plates (*O. patersoni*) and tentacle scales are also absent; (4) the structure of oral papillae is primitive; (5) the genital cleft is not noticeable; (6) the body size is small.

On the other hand, the new species have characters that constitute a specialization among Ophiurinae: (1) the presence of skin covered patches on the disk and arms; (2) the presence of a large terminal plate; (3) the wide separation between the lateral plates of each arm segment on the dorsal side; (4) the absence of dorsal plates on the arms; (5) the presence of thin skin in the place of the dorsal plates through which the vertebrae can be seen; (6) the presence of widened cap-like terminal plate resembling those plates that were found in *Ophiambix meteoris* Bartsh, 1983, a representative of an extremely specialized genus. The absence of dorsal plates and their replacement by the skin are interpretated as a resorbtion of the plates (Hotchkiss 1993).

On the basis of their plesiomorphic and apomorphic characteristics the *Ophiuraster* species have clear affinities to the Ophiurinae such as *Ophiambix*, *Astrophiura* and *Ophiophycis*, which superficially resemble sea-stars. But this similarity with asteroids has been reached by different ways in different genera.

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Une nouvelle espèce de *Molineus* (Nematoda, Trichostrongylina, Molineoidea), parasite d'un Primate sud-américain

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RÉSUMÉ
Molineus midas n.sp., parasite de l'intestin grêle de *Saguinus midas* (Primate, Hapalidae) en Guyane française est décrite ici. Les nombreuses espèces du genre, décrires chez les Carnivores dans le monde entier, ont trois caractères primitifs fréquents chez les Strongylina, mais rares chez les Trichostrongylina, à savoir : une bourse caudale de type 2-1-2, des côtes 4 courtes et un sillon transversal au niveau du pore excréteur. L'un ou l'autre de ces caractères manque chez les espèces parasites de Singes américains ou chez les espèces géographiquement proches de la Guyane. Ces trois caractères sont absents chez la nouvelle espèce.

MOTS CLÉS
Molineus midas n.sp., Nematoda, Trichostrongylina, Molineoidea, *Saguinus*, Guyane française.

ABSTRACT
A new Molineus *species (Nematoda, Trichostrongylina, Molineoidea), parasite of a South American primate.* Description of *Molineus midas* n.sp., a parasite of the small intestine of *Saguinus midas* (Primate, Hapalidae) from French Guyana. The many species of the genus, parasites of Carnivora throughout the world, have three primitive characters frequently occurring in Strongylina but rarely in Trichostrongylina. These characters are the following: a pattern bursa of 2-1-2, rays 4 short and a cervical groove at the level of the excretory pore. One or other of these characters is lacking in the species parasitic in American primates or in the species geographically close to Guiana. These three characters are absent in the new species.

KEY WORDS
Molineus midas n.sp. Nematoda, Trichostrongylina, Molineoidea, *Saguinus*, French Guiana.

INTRODUCTION

Le genre *Molineus,* créé par Cameron (1923) et redéfini par Durette-Desset & Chabaud (1981b), se rencontre chez des Carnivores dans le monde entier, sauf l'Australie, et chez des Primates néotropicaux. Il est intéressant car il est morphologiquement très proche du genre *Oswaldocruzia* Travassos, 1937, parasite d'Amphibiens et de Reptiles. La plupart des espèces montrent en effet des caractères archaïques qui se rencontrent chez de nombreux Strongylida, mais très rarement chez les Trichostrongylina.
L'espèce trouvée chez un Primate Hapalidae *Saguinus midas* (Linné, 1758) en Guyane française et décrite ci-dessous, est originale du fait qu'elle ne possède aucun de ces caractères primitifs.

MATÉRIEL ET MÉTHODES

Le matériel a été étudié selon les méthodes classiques et éclairci dans le lactophénol si nécessaire. La nomenclature utilisée au-dessus du groupe famille est celle de Durette-Desset & Chabaud (1995). Le synlophe est étudié selon la méthode de Durette-Desset (1985). La nomenclature utilisée pour l'étude de la bourse caudale est celle de Durette-Desset & Chabaud (1981a).
Les spécimens-types ont été déposés dans les collections du Muséum national d'Histoire naturelle, Paris (MNHN).

SYSTÉMATIQUE

Genre *Molineus* Cameron, 1923

Molineus midas n.sp.
(Fig. 1)

MATÉRIEL-TYPE. — ♂ holotype, ♀ allotype (MNHN195KHa), 3 ♂♂ et 3 ♀♀ paratypes (MNHN195KHb).

LOCALITÉ-TYPE. — Guyane française, rivière Aratay, à 80 kms de la côte, 19.XI.1980.

HÔTE. — *Saguinus midas* (Linné, 1758) (Primate, Simioidea).

LOCALISATION. — Intestin grêle.

AUTRE MATÉRIEL ÉTUDIÉ. — 7 ♂♂, 16 ♀♀, 6 parties postérieures et 2 parties antérieures, l'ensemble MNHN196KH. Même espèce-hôte, même région, même date de récolte.

DESCRIPTION
Trichostrongle de taille moyenne dont le corps est déroulé. Pore excréteur et deirides situés juste en arrière de l'anneau nerveux. Absence de sillon excréteur. Vésicule céphalique présente.

Synlophe (étudié chez un mâle et une femelle)
Chez les deux sexes, le corps est parcouru longitudinalement par quatorze crêtes cuticulaires longitudinales dépourvues de soutien chitinoïde. En coupe transversale, au milieu du corps, on compte cinq crêtes ventrales, cinq dorsales, deux latérales gauches et deux latérales droites (Fig. 1D, E). Les crêtes sont de petite taille et orientées perpendiculairement à la paroi du corps. Elles prennent naissance en arrière de la vésicule céphalique et se terminent en avant de la bourse caudale chez le mâle et à environ 60 µm en avant de la pointe caudale chez la femelle.

Mâle holotype
Long de 3200 µm sur 65 µm de large dans sa partie moyenne. Vésicule céphalique haute de 45 µm sur 25 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 140 µm, 160 µm et 170 µm de l'apex. Œsophage long de 340 µm (Fig. 1A).
Bourse caudale symétrique de type 2-1-2 avec une ornementation épineuse sur les lobes latéraux, principalement entre la paroi du corps et les côtes 6. Papilles prébursales non observées. Côtes 4 très courtes. Leurs extrémités sont plus proches de celles des côtes 3 que de celles des côtes 5. Côtes 8 naissant presqu'à la racine de la côte dorsale ; côte dorsale divisée dans son tiers distal en deux branches, une branche externe (côte 9) et une branche interne qui se divise distalement en deux rameaux (côte 10 et phasmides). Cône génital peu développé, portant sur sa lèvre antérieure la papille zéro arrondie et sur sa lèvre postérieure deux minuscules papilles 7 (Fig. 1J).

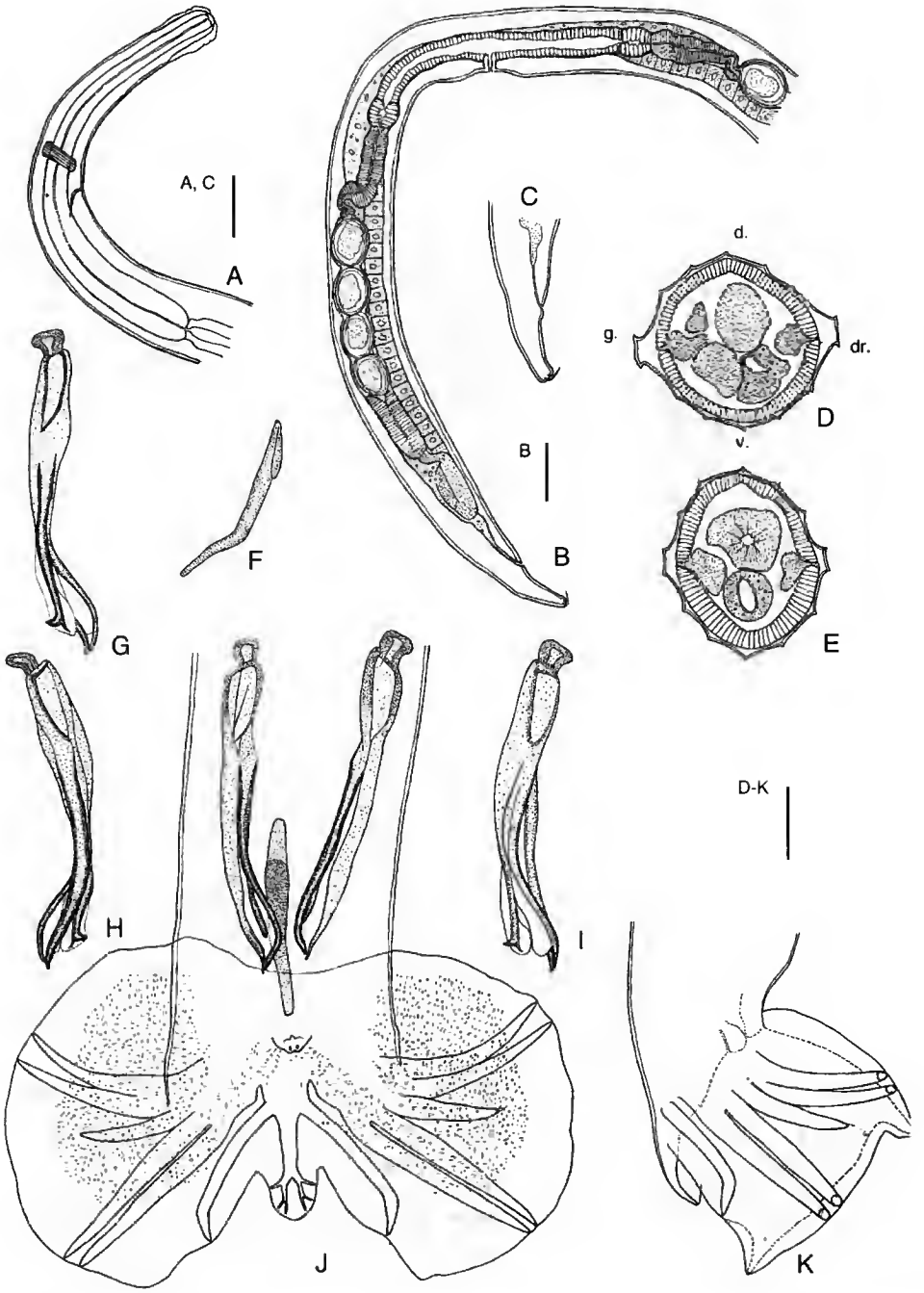

Fig. 1. — *Molineus midas* n.sp. ; **A**, ♂, extrémité antérieure, vue latérale droite ; **B**, ♀, extrémité postérieure, vue latérale droite ; **C**, ♀, queue, vue latérale droite ; **D**, **E**, synlophe ; **D**, ♀, au milieu du corps ; **E**, ♂, au milieu du corps ; **F**, ♂, gubernaculum, vue latérale gauche ; **G-I**, ♂, spicule gauche disséqué ; **G**, vue dorsale ; **H**, vue externo-latérale ; **I**, vue ventrale ; **J**, **K**, bourse caudale ; **J**, vue ventrale ; **K**, vue latérale droite. Les coupes sont orientées comme la figure D : **d**, dos ; **v**, ventre ; **g**, gauche ; **dr**, droite. Échelles : A, C, 50 µm ; B, 60 µm ; D-K, 30 µm.

Spicules longs de 120 µm, divisés en trois branches : une branche externo-latérale et deux branches internes. Les extrémités des branches externo-latérale et interno-ventrale sont pointues, celle de la branche interno-dorsale est en forme de marteau (Fig. 1G-I). Gubernaculum incurvé, haut de 70 µm en vue latérale (Fig. 1F).
Dimensions des trois mâles paratypes, longueur : 3250-3450-3600 µm, largeur 70-70-60 µm ; vésicule céphalique haute de 45-50-55 sur 30-30-30 µm de large ; anneau nerveux, pore excréteur et deirides situés respectivement à 130-165-140 µm, 140-175-150 µm et 145-190-160-µm de l'apex ; œsophage long de 340-370-340-µm ; spicules longs de 135-135-120 µm et gubernaculum haut de 70-70-70 µm.

Femelle allotype
Longue de 3700 µm, large de 70 µm dans sa partie moyenne. Vésicule céphalique haute de 50 µm sur 30 µm de large. Anneau nerveux, pore excréteur et deirides situés respectivement à 150, 170 et 190 µm de l'apex. Œsophage long de 410 µm.
Didelphie : vulve s'ouvrant à 660 µm de la pointe caudale, soit au sixième postérieur du corps. *Vagina vera* de 20 µm partageant le vestibule long de 270 µm en deux parties égales. Branche génitale antérieure : sphincter, trompe et branche utérine longs respectivement de 30, 20 et 480 µm. Branche génitale postérieure : sphincter, trompe et branche utérine longs respectivement de 23, 20 et 300 µm. Branche utérine antérieure contenant six œufs et postérieure quatre (Fig. 1B). Œufs au stade morula, hauts de 50 µm sur 30 µm de large. Queue longue de 60 µm avec une pointe caudale de 12 µm (Fig. 1C).
Dimensions des trois femelles paratypes, longueur : 3750-3950-3900 µm ; largeur 70-70-70 µm ; vésicule céphalique haute de 50-45-50 sur 30-30-30 µm de large ; anneau nerveux, pore excréteur et deirides situés respectivement à 140-140-135 µm, 160-165-150 µm et 160-170-165 µm de l'apex ; œsophage long de 400-370-350 µm ; vulve s'ouvrant à 660-770-750 µm de la pointe caudale ; ovéjecteur : 321-357-346 µm ; branche utérine antérieure : 470-410-550 µm avec 6-3-3 œufs ; branche utérine postérieure : 330-350-330 µm avec 4-1-3 œufs ; queue longue de 70-80-80 µm avec une pointe caudale de 12-12-12 µm.

Discussion

Les spécimens décrits ci-dessus appartiennent au genre *Molineus* Cameron, 1923 (Molineoidea) dont ils possèdent les principaux caractères : synlophe avec crêtes orientées perpendiculairement à la paroi du corps, bourse caudale avec côtes 4 courtes, côtes 2 et 3 d'une part, côtes 5 et 6 de l'autre, proches et parallèles, spicules courts et épais, femelle didelphe avec vestibule allongé et trompe très courte.
Les spécimens du *Saguinus* se distinguent immédiatement de toutes les autres espèces du genre par des côtes 8 longues, atteignant le bord de la bourse caudale. Il s'agit donc d'une nouvelle espèce que nous nommons *Molineus midas* n.sp., en référence au nom d'espèce de l'hôte.
Trois caractères primitifs sont présents chez de nombreux Strongylina et disparaissent chez presque tous les Trichostrongylina :
1. La bourse caudale de type 2-3, c'est-à-dire avec les côtes 2 et 3 constituant un groupe séparé du groupe formé par l'ensemble des côtes 4, 5 et 6. L'évolution se fait par une migration des papilles 4 vers l'avant, ce qui conduit à une bourse caudale de type 2-1-2, puis finalement à un type 3-2 (voir Durette-Desset & Chabaud, 1981a) ;
2. Les côtes 4 très courtes se terminant loin du bord de la bourse caudale ;
3. Le pore excréteur s'ouvrant au fond d'un profond sillon transversal.
Il est intéressant de suivre l'évolution de ces trois caractères dans le genre *Molineus* selon la répartition géographique et selon l'hôte.
Neuf espèces sont connues en zone holarctique : *M. patens* (Dujardin, 1845) ; *M. europaeus* Zunker, 1928 ; *M. petrovi* Durette-Desset *et* Pesson, 1987 (= *M. patens* sensu Petrov, 1928) ; *M. americanus* Sprehn, 1932 ; *M. barbatus* Chandler, 1942 ; *M. mustelae* Schmidt, 1965 ; *M. samueli* Platt *et* Pence, 1981 ; *M. legerae* Durette-Desset *et* Pesson, 1987 et *M. springsmithi yayeyamanus* Hasegawa, 1989. À l'exception de *M. petrovi* chez laquelle le sillon excréteur n'est pas décrit et de *M. americanus* insuffisam-

ment connue, toutes les espèces possèdent les trois caractères primitifs réunis.

Trois espèces sont connues en zone éthiopienne : *M. genettae* (Cameron, 1927) ; *M. cynictis cynictis* (Le Roux, 1933) ; *M. cynictis thosi* Troncy, 1970. Elles possèdent aussi les trois caractères primitifs réunis.

Les trois espèces orientales, *M. planicipitis* (Cameron, 1928), *M. springsmithi* Inglis *et* Ogden, 1965 et *M. inglisi* Durette-Desset *et* Pesson, 1987 (= *M. patens* sensu Inglis *et* Ogden, 1965) sont primitives par la longueur de la côte 4 et par la présence du sillon excréteur, mais toutes trois ont une bourse de « type 2-3 » tendant au « type 2-1-2 ». L'espèce décrite aux Philippines, *M. asiaticus* Tubangui *et* Masilungan, 1937, est du « type 2-1-2 ».

En région néotropicale, sept espèces sont connues chez les Carnivores et trois chez les Primates. Les sept espèces parasites de Carnivores, *M. felineus* Cameron, 1923, *M. barbaris* Cameron, 1936, *M. major* Cameron, 1936, *M. pardalis* Cameron, 1936, *M. paraensis* Travassos, 1937, *M. nasuae* Lent *et* Freitas, 1938 et *M. brachiurus* Costa *et* Freitas, 1967 possèdent des côtes 4 courtes, six d'entre elles ont un sillon excréteur et seule *M. paraensis* en est dépourvue. Trois espèces (du Brésil) ont une bourse caudale de type 2-3 et quatre (une du Brésil et trois de la Trinité) de type 2-1-2.

Les trois espèces de Primates déjà connues, *M. torulosus* (Molin, 1861), *M. elegans* Travassos et Darriba, 1929 et *M. vexillarius* Dunn, 1961 ont des côtes 4 courtes et un sillon excréteur présent, mais toutes trois ont une bourse caudale de type 2-1-2 tendant au type 3-2. L'espèce décrite ci-dessus partage avec les autres espèces de Primates une bourse caudale de type 2-1-2 tendant au type 3-2, des côtes 4 courtes, mais elle est la seule à être dépourvue de sillon excréteur.

En résumé, le genre *Molineus* conserve des caractères primitifs, de type Strongylina, chez les Carnivores du monde entier. Une évolution morphologique vers un type plus spécialisé n'aurait eu lieu que, soit dans une zone géographique très limitée (nord du Brésil, Guyane, île de la Trinité), soit chez les Primates. L'espèce décrite ci-dessus, cumulant ces deux particularités, paraît être la plus spécialisée actuellement connue.

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A study in medical history: introduction of medicinal leeches into the West Indies in the nineteenth century

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ABSTRACT

Medicinal leeches were not found in the West Indies prior to 1822, but by the turn of the century, a large, aggressive leech abounded on Puerto Rico, St Lucia, Martinique and other islands. The authors conclude that this "Caribbean leech", described as *Hirudinaria* (*Poecilobdella*) *blanchardi* Moore, 1901, is a junior synonym of the "buffalo" leech *Hirudinaria manillensis* (Lesson, 1842), the medicinal leech of India and neighbouring countries of South-East Asia. The final proof of the true identity of this West Indian leech came from comparison of the nucleotide sequences of the cDNAs of the hirudin polypeptide from leeches from St Lucia and from Bangladesh. The authors present evidence that this leech arrived from ships carrying labourers from colonial India starting in the mid-1840's. Each of these ships were required to have leeches on board for medicinal purposes. During this study, the existence of a second introduced leech species in the West Indies was unexpectedly discovered, in Guadeloupe. The question remains open whether this second species is the medicinal leech intentionally introduced into Guadeloupe from Senegal by the French for breeding purposes in the 1820's.

KEY WORDS
Hirudinea,
Hirudinaria,
hirudin,
medicinal leech,
medical history,
West Indies.

RÉSUMÉ

Une étude d'histoire de la médecine : l'introduction des sangsues médicinales aux Antilles au dix-neuvième siècle. Les sangsues médicinales n'avaient jamais été rencontrées aux Antilles avant 1822, mais à la fin du siècle, une sangsue agressive, de grande taille, était abondante à Porto Rico, Sainte-Lucie, en Martinique ainsi que dans d'autres îles. La conclusion des auteurs est que cette « sangsue des Caraïbes » décrite comme *Hirudinaria* (*Poecilobdella*) *blanchardi* Moore, 1901 est un synonyme junior de *Hirudinaria manillensis* (Lesson, 1842), la sangsue médicinale d'Inde et des régions voisines du Sud-Est asiatique. La preuve définitive de la véritable identité de cette sangsue des Antilles est apportée par la comparaison des séquences de nucléotides du cDNA du polypeptide de l'hirudine des sangsues provenant de Sainte-Lucie et du Bangladesh. Les auteurs démontrent que cette sangsue est arrivée par les navires transportant la main-d'œuvre en provenance de l'Inde coloniale à partir du milieu des années 1840. Chaque navire devait avoir des sangsues à bord, à des fins médicinales. Au cours de cette étude, l'existence d'une deuxième espèce de sangsue introduite aux Antilles a été découverte en Guadeloupe. La question demeure de savoir si cette seconde espèce est bien la sangsue médicinale du Sénégal introduite intentionnellement en Guadeloupe par les Français dans les années 1820.

MOTS CLÉS
Hirudinea,
Hirudinaria,
hirudine,
sangsue médicinale,
histoire de la médecine,
Antilles.

INTRODUCTION

The introduction of a new animal or plant species can have profound consequences, especially on islands and other isolated ecosystems. Many of such introductions have occurred, but usually unrecorded, during the 300 years of active European colonisation when there were mass movements of people and materials to and from the New World. For example, yellow fever along with the mosquito *Aedes aegypti* (Linn.) was introduced into the Caribbean and other parts of the neotropical region aboard slave ships from West Africa in the seventeenth century (Taylor 1971). Clearly, it is of general interest for future environmental impact assessments to identify specific examples of heretofore unrecognised introductions of other bloodsucking animals. We document in this paper a rare example of the introduction of a medicinal leech into the West Indies in the nineteenth century and give evidence of yet another introduced leech.

On certain islands of the eastern Caribbean there abounds today a large medicinal leech species widely known as *Caribeobdella blanchardi*. It was described nearly a century ago and presumed to be unique to the New World (Moore 1901; Ringuelet 1976), having no near relatives whatsoever in the Western Hemisphere (Sawyer & Kinard 1980; Sawyer 1986: 736). In this multidisciplinary paper, we present molecular, morphological and taxonomic evidence for the first time that this remarkable West Indian species is in fact identical to *Hirudinaria manillensis* (Lesson, 1842), the medicinal leech of India and neighbouring countries of South-East Asia. In addition, we discovered in Guadeloupe that a leech also known by the specific name *blanchardi* represents an undetermined species of *Asiaticobdella* of African/Indian origin.

Current systematics recognises six species of "buffalo" leeches in the Hirudinariinae, a subfamily of the Hirudinidae characterised by the presence of a large vaginal caecum ("caecal pouch") in the female reproductive system (Sawyer 1986: 683-687). These six species are divided into two genera which are differentiated as follows: in *Poecilobdella*, the female reproductive system has a distinct "vagina" (termed "vaginal stalk" by some workers) and the male system lacks ejaculatory bulbs (Fig. 1B); whereas in *Hirudinaria*, the female system lacks an elongate "vagina" and the male system has ejaculatory bulbs (Fig. 1A). Five species occur naturally throughout tropical and

subtropical Asia from the western limit of the Indian subcontinent to the Pacific coast including numerous islands and archipelagoes. The sixth nominal species, "*Caribeobdella blanchardi*", was first described as being from Puerto Rico as *Hirudinaria* (*Poecilobdella*) *blanchardi* by Moore (1901).

We also address in this paper the question of when these leeches were introduced into the West Indies and by what mechanism(s). We document that no native medicinal leeches lived in the West Indies prior to 1822. Furthermore, there is no record of the existence of any leech resembling *Hirudinaria* on any of the West

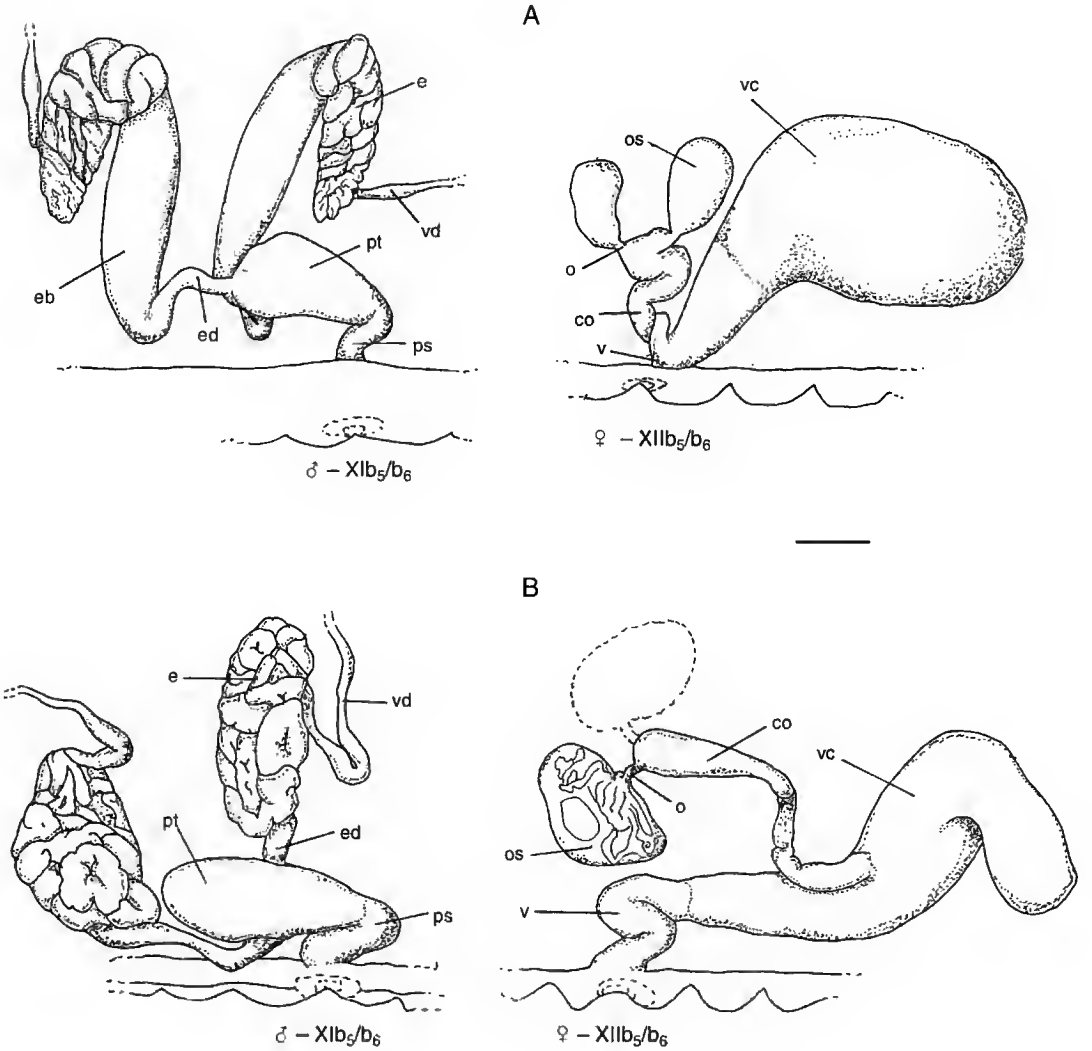

FIG. 1. — Comparison of taxonomically diagnostic features of the male (left) and female (right) reproductive systems of the two genera of "buffalo" leeches, *Hirudinaria* and *Poecilobdella*. **A**, *Hirudinaria manillansis* from St Lucia (the Martinique leech is the same, unillustrated); **B**, *Poecilobdella granulosa* from a dealer in "Madras area", India. See "Methods" for specific localities. **co**, common oviduct; **e**, epididymis; **eb**, ejaculatory bulb; **ed**, ejaculatory duct; **o**, oviduct; **os**, ovisac; **ps**, penis sheath; **pt**, prostate; **v**, "vagina" *sansu lato* (portion between common oviduct and female gonopore); **vc**, vaginal caecum; **vd**, vas deferens. Scale bar: 1 mm. Viewed from the left side, anterior to left. Note both species have a well-developed vaginal caecum.

Indian islands prior to 1827. However, starting in the mid-1840's ships taking emigrant labourers from India to various British and French islands of the West Indies were required to have leeches on board for medicinal purposes. Over a period of several decades these emigrant ships took on thousands of the Indian medicinal leech *Hirudinaria*, primarily at Calcutta and Madras. We conclude that, about the late 1840's, some of these leeches were released onto one or more islands and that their descendants are the leeches thriving today on St Lucia, Puetto Rico, Martinique and other islands. The capability of medicinal leeches to colonize very rapidly areas where similar species do not occur has been documented in Guadeloupe (Pointier *et al.* 1988).

Early records of medicinal leeches in the West Indies

The earliest account of medicinal leeches in the West Indies appears to be a report in 1817 by Dr John Williamson who recorded: "Practitioners in the West Indies labour under a great disadvantage, by not having leeches in that country. They have been sent there at a great expense; but they soon became sickly, and perished" (Williamson 1817: 361). The absence of leeches was later corroborated in 1822 by M. J. Achard, Government Pharmacist at Port Royal, Martinique, who recorded that there were no native species of leeches in Martinique which could be used therapeutically (Achard 1825). In 1827, however, Blainville tantalizingly described from Martinique a 4 cm leech with blood in its crop and other features of the Hirudinidae (Blainville 1827: 250; Moquin-Tandon 1846: 324). In 1893 Raphael Blanchard of Paris, the foremost leech taxonomist at that time, reported without further detail there was a species of "*Hirudinaria*" on Martinique, "whose presence in the Antilles is a real curiosity". In 1897 Blanchard went on to say, in reference to a discussion of "*Hirudinaria* (*Poecilobdella*) *granulosa*", an Asian species: "Also it is very interesting to find it in the Antilles, where it has been, without doubt, transported by man for medicinal purposes; discarded in the streams where it has acclimated. It is found in abundance in Martinique, where it is very prospetous [...]. We have received numerous live animals, in two batches [...]. One batch sent in 1891 by P. Vanhaecke, Superior du Séminaite-Collège de Fort de France [...]. In 1893 we received some from another source, one of which was very large, 245 mm in length. We know only by hearsay that it occurs on islands other than Martinique [...]." In 1901, a similar leech was described as a new species *Hirudinaria* (*Poecilobdella*) *blanchardi* by the eminent taxonomist J. Percy Moore of Philadelphia, from specimens from Puetto Rico. In 1934, Oka obtained specimens of the Martinique leech and compared it externally with what he considered to be the same species from Taiwan.

Early attempts to establish leeches in the West Indies

During the colonial period the medicinal leech *Hirudo medicinalis* Linnaeus, 1758 was very widely used for medicinal purposes throughout Europe, including their colonies (Sawyer 1981). From the beginning of the nineteenth century, medicinal leeches had become increasingly rare in Western European countries, most notably France and England, and had to be imported in large numbers to meet an enormous demand. In a single year, 1832, more than fifty-seven millions leeches were imported into France where they were used mainly in hospitals in the vicinity of Paris. Customs records document that during the nineteenth century more than one billion leeches were imported into France alone from eastern parts of Europe (Sawyer 1981). (Today *Hirudo medicinalis* is listed as an endangered species and accordingly protected worldwide by the CITES convention. While overcollection undoubtedly played a significant role, a full understanding of the factors underlying the decline of this and potentially other medicinal leech species worldwide is problematical).

In the meanwhile demand for medicinal leeches in the New World was growing faster than supply. Although the United States had its own native leech species, *Macrobdella decora* (Say, 1824), sometimes called the "American medicinal leech", it was generally recognized as inferior in that it made a more shallow bite and bled much

less (*e.g.* Wood & Bache 1867: 442). We now know the subfamily Macrobdellinae. *Macrobdella* Verrill, 1872 and allies endemic to North and South America have very reduced bleeding times compared with the true medicinal leeches *Hirudo medicinalis* and *Hirudinaria manillensis* of the Eastern Hemisphere (Munro *et al.* 1991), hence the need for the American colonisrs to import leeches. Accordingly, large numbers of *H. medicinalis* were imported into the United States from Europe throughout the eighteenth and nineteenth centuries and especially in the period before the American Civil War (Hagy 1991). Because of chronic supply and transportation problems, several serious attempts were made to breed *H. medicinalis* in the United States (Hessel 1881, 1884) but all such efforts failed. The same unsuccessful scenario also took place in the French West Indies.

Since the West Indies in the early nineteenth century did not have any native medicinal leeches, they were entirely dependent upon importation from abroad. At the time the French Antilles were, as was France itself, leech "manic" and had been importing thousands of *H. medicinalis* from Europe since at least 1814 (Achard 1825). On at least one occasion in 1822 the Antilles had even imported leeches, undoubtedly *Macrobdella decora*, from "Newfoundland" (Anonymous 1822).

In order to satisfy increasing demand, the French medical authorities, as early as 1822, made serious attempts to breed *Hirudo* in the French Antilles (Anonymous 1824; Achard 1825), including French Guyana on mainland South America (Conseil de Santé 1831). These attempts at breeding *Hirudo* are documented in various reports in the *Annales maritimes et coloniales* during the 1820's and early 1830's (see Berget & Rey 1874 for full bibliography) but were all unsuccessful.

In 1829 leeches were imported from the French colony of Senegambia in West Africa into the Antilles (*e.g.* Dupuy 1830; Calve 1830). The exact species involved is unclear (see Discussion). In any evenr, the leech species the authors of this paper collected in abundance in St Lucia, Martinique and Puerto Rico are disrincrly members of the Hirudinariinae, a well-characterised subfamily which does not live in Africa. The bloodsucking ("hirudinid") leeches of Africa are very unlike *Hirudinaria manillensis*. No African leech, for example, has a "vaginal caecum" so characteristic of the Asian Hirudinariinae (Sawyer 1986: 684); however, we leave open the possibility that a leech species found today on Guadeloupe is of African origin (see Discussion).

By way of summary, during the 1820's the French imported three species of leeches into the French Antilles, including French Guyana. These were *Hirudo medicinalis* from Europe, *Macrobdella decora* from Newfoundland, and an unidentified hirudinid from Senegambia. None of these species represent the large leech *Hirudinaria manillensis* we collected in St Lucia, Martinique and Puerto Rico.

MATERIALS AND METHODS

Materials

We sampled accessible streams and ponds by slowly wading into the water, disturbing rhe mud in the process. Leeches were collected by hand or net while they swam near the water surface or while they attached to the bare legs of the collectors. Leeches were either taken alive to the laboratory for breeding and further studies or were preserved under field conditions with 5% formalin or 70% ethanol for later dissection and identification.

We examined preserved specimens from the Caribbean and from Asia in rhe Smithsonian Institution (Washington), Natural History Museum (London), Muséum narional d'Histoire naturelle (Paris) and Institute for Zoological Taxonomy, Zoology Museum, University of Amsterdam. However, owing to uncertainties of labelling and constraints on dissecting old museum material, conclusions herein are based on specimens recently collected alive from nature by the authors or recently by colleagues.

Preserved specimens were pinned under alcohol and dissected from dorsal midline to reveal diagnostic features of male and female reproductive systems. The drawings were made freehand with the aid of an ocular micromerer. Ar leasr two mature specimens were dissected from each loca-

lity wherever possible. Dissected specimens are presently in the personal collection of the second author but will eventually be lodged with the Natural History Museum (London) and the Smithsonian Institution (Washington). Specimens of leeches collected alive in St Lucia, Martinique and Puerto Rico were examined externally in detail and then carefully dissected by F. O. P. Hechtel. Each was compared with specimens collected in Bangladesh, India, Philippines and other parts of Asia. The systematics follows that of Sawyer (1986). Sawyer (1986: 683) inadvertently stated that the Hirudinariinae have pharyngeal ridges terminating independently between the jaws. This not the case for any Hirudinariinae examined by us in the West Indies nor in Asia.

MOLECULAR GENETICS

To establish if the leech collected in St Lucia was identical to *Hirudinaria manillensis*, a genetic comparison was made of specimens from St Lucia with specimens from an Asian population of *H. manillensis*. Although *H. manillensis* occurs throughout South-East Asia we chose for this study leeches of this species from Bengal from which, according to historical evidence presented below, the West Indies leeches probably originated. We chose a population from Sylhet, Bangladesh, because it had been the basis of a prior molecular study (Scacheri *et al.* 1993). Toward this end arrangements were made to ship live specimens of *Hirudinaria manillensis* collected from Bangladesh to the laboratory of Biopharm (UK) Ltd in Wales. Similarly, Sawyer collected specimens from St Lucia in 1989 and maintained them alive in Wales. In 1990 Sawyer took live individuals from each population to the laboratory of the fourth author E. Scacheri, in Milan, Italy. Individual heads were dissected from the bodies, washed in 5 M NaCl, and quickly frozen in liquid nitrogen prior to storage at – 80 °C.

Total cellular RNA was prepared from leech heads essentially as described by Harvey *et al.* (1986). The reverse transcriptase reaction was carried out in a 40 µl volume as follows: 10 µg total RNA from leech heads was mixed with 1 µg oligo(dT) primer, 8 µl 5 mM dNTP mix and 8 µl reverse transcriptase buffer (250 mM Tris/HCl pH 8.3, 300 mM KCl, 50 mM MgCl2, 5 mM dithiothreitol), heated to 65 °C for 2 min and quickly chilled on ice. 10 U RNasin (Promega) and 20 U avian myeloblastosis virus reverse transcriptase (Boehringer Mannheim) were added, and the tube was incubated at 42 °C for 2 hours. The reaction mixture was phenol/chloroform-extracted, isopropanol-precipitated and resuspended in 60 µl sterile distilled water. Oligonucleotide primers were synthesized on an Applied Biosystems model 380B DNA synthesizer. To obtain the complete sequence of HM1 cDNA, three rounds of PCR amplification were performed. Amplified products were analyzed on 1.5% agarose gel, phenol-purified and ethanol-precipitated. For further details see Scacheri *et al.* (1993).

HISTORICAL RESEARCH

During the course of this study, we identified that the species from St Lucia, Martinique and Puerto Rico probably originated from the Indian subcontinent sometime in the last century. Accordingly, the question arose as to how and when the leech could have been imported from that far away region. The historical archives of this period in the Oriental and India Office Library, Blackfriars Road, London, and the Colonial Office (CO) records of the Public Record Office (PRO), Kew, London, were a rich source of information. Much of this archival research was conducted with the invaluable assistance of Mrs Betty Thomson, Richmond, Surrey. The third author J. W. Hagy documented the importation of leeches into the French West Indies in the 1820's, using archives of the British Library, London, as well as the Interlibrary resources of the University of Charleston. With funding from the University of Charleston, Hagy focussed on Indian emigration archives of the 1840's at the Oriental and India Office Library, London. Our research eventually focussed on the mass movement of indentured labourers in the 1840's from India following the emancipation of slaves on the West Indian islands. Archival evidence is presented below which documents that leeches regularly accompanied these labourers

HM1 St Lucia	TCAAAAG	ATG	TTC	TCT	CTC	AAG	TTG	TTC	GTT	GTC	TTC	CTG	
Amino acids		Met	Phe	Ser	Leu	Lys	Leu	Phe	Val	Val	Phe	Leu	
HM1 Bangladesh		ATG	TTC	TCT	CTC	AAG	TTG	TTC	GTT	GTC	TTC	CTG	
									↓				
HM1 St Lucia	GCT	GTT	TGC	ATC	TGC	GTG	TCT	CAA	GCA	GTG	AGC	TAC	ACT
aa	Ala	Val	Cys	Ile	Cys	Val	Ser	Gln	Ala	Val	Ser	Tyr	Thr
HM1 Bangladesh	GCT	GTT	TGC	ATC	TGC	GTG	TCT	CAA	GCA	GTG	AGC	TAC	ACT
	5					10					15		
HM1 St Lucia	GAT	TGT	ACG	GAA	TCA	GGC	CAG	AAT	TAT	TGT	CTA	TGC	GTG
aa	Asp	Cys	Thr	Glu	Ser	Gly	Gln	Asn	Tyr	Cys	Leu	Cys	Val
HM1 Bangladesh	GAT	TGT	ACG	GAA	TCA	GGC	CAG	AAT	TAT	TGT	CTA	TGC	GTG
			20					25					30
HM1 St Lucia	GGA	GGT	AAT	CTC	TGC	GGT	GGA	GGC	AAA	CAT	TGT	GAA	ATG
aa	Gly	Gly	Asn	Leu	Cys	Gly	Gly	Gly	Lys	His	Cys	Glu	Met
HM1 Bangladesh	GGA	GGT	AAT	CTC	TGC	GGT	GGA	GGC	AAA	CAT	TGT	GAA	ATG
					35					40			
HM1 St Lucia	GAC	GGT	TCT	GGA	AAT	AAA	TGC	GTC	GAT	GGG	GAA	GGT	ACT
aa	Asp	Gly	Ser	Gly	Asn	Lys	Cys	Val	Asp	Gly	Glu	Gly	Thr
HM1 Bangladesh	GAC	GGT	TCT	GGA	AAT	AAA	TGC	GTC	GAT	GGG	GAA	GGT	ACT
		45					50					55	
HM1 St Lucia	CCG	AAG	CCT	AAG	AGC	CAG	ACT	GAA	GGC	GAT	TTC	GAA	GAA
aa	Pro	Lys	Pro	Lys	Ser	Gln	Thr	Glu	Gly	Asp	Phe	Glu	Glu
HM1 Bangladesh	CCG	AAG	CCT	AAG	AGC	CAG	ACT	GAA	GGC	GAT	TTC	GAA	GAA
				60					65				
HM1 St Lucia	ATC	CCA	GAT	GAA	GAT	ATA	TTG	AAT	TAA	CGAACGCATAT			
aa	Ile	Pro	Asp	Glu	Asp	Ile	Leu	Asn	End				
HM1 Bangladesh	ATC	CCA	GAT	GAA	GAT	ATA	TTG	AAT	TAA	CGAACGCATAT			

FIG. 2. — Comparison of the nucleotide and deduced amino acid sequences of the cDNAs of the hirudin polypeptide variant HM1 from leeches from St Lucia and from Sylhet, Bangladesh. The arrow points to the signal peptidase cleavage site. The deduced amino acid sequence corresponds to the complete amino acid sequence determined from leeches from Bangladesh by peptide mapping analysis published elsewhere (Scacheri *et al.* 1993).

aboard ship for medical purposes on the long journey from India to the West Indies.

Since Mauritius in the southern Indian Ocean was a common port of call for such ships, Sawyer searched through selected back issues of the colonial newspaper *Le Cernéen, Journal de L'Île Maurice*, from 1833 to 1872 looking for evidence for the importation of leeches into this island during this period. This research was conducted in the reading room of the National Archives, DBM Complex, Petite Rivière, Mauritius.

RESULTS

TAXONOMY OF LEECHES FROM PUERTO RICO, MARTINIQUE AND ST LUCIA

Hirudinaria manillensis, the most common and widespread of the "buffalo" leeches of Asia, was originally described as being from the Philippine island of Luzon by Lesson (1842) (see also Harding & Moore 1927). In 1986, Hechtel collected specimens from this same island. Figure 3A shows the large vaginal caecum characteristic of the Hirudinariinae, as well as the presence of ejaculatory bulbs and absence of an elongate "vagina" characteristic of the genus *Hirudinaria*. Following detailed morphological examination, numerous specimens obtained from Bangladesh proved unequivocally to be *Hirudinaria manillensis* (Fig. 3B). [Hechtel noted that *Hirudinaria manillensis* is polymorphic, occurring in two main colour phases: a green phase (darkish green dorsum and paler green venter) and a reddish phase (dark reddish brown dorsum and paler brick-red venter). Though both phases occur together, at least in Asia, one phase predominates overwhelmingly in each population.]

The type specimens of *Hirudinaria* (*Poecilob-*

della) *blanchardi* could not be located and are presumed lost. This being the case, dissections (Fig. 3C) of specimens collected live from Puerto Rico revealed no significant differences between them and the Luzon and Bangladesh leeches. Specimens collected later from St Lucia (Fig. 1A) and Martinique (not illustrated) also proved to be the same species. Specimens from Puerto Rico, Martinique and St Lucia all possess the large vaginal caecum, ejaculatory bulbs and lack an elongate "vagina". On morphological grounds, we have no hesitation in assigning medicinal leeches of these three islands to the species *Hirudinaria manillensis*.

Molecular studies focussed on an inter-population comparison of the genomic organisation of the leech polypeptide hirudin, a well-characterised inhibitor of thrombin. As part of another study the thrombin inhibitor secreted by *H. manillensis* from the Bangladesh population was partially purified (Electricwala *et al.* 1991). Two variants were eventually found and sequenced, called HM1 and HM2, differing in ten amino acids in the central part of the molecule (Scacheri *et al.* 1993). The protein structure of the two hirudin variants include sixty-four amino acids with six cysteine residues, plus twenty residues which constitute the signal peptide required for extracellular secretion. This signal peptide is identical in both isoforms. Based on this structural information Scacheri and her colleagues were able to isolate cDNAs for both HM1 and HM2 by extraction of leech head RNA, subsequent DNA synthesis and PCR amplification. Furthermore, by cloning the genomic fragments of both variants they were able to elucidate for the first time the gene organisation of hirudin-like antithrombins from leeches (Scacheri *et al.* 1993). Fully active recombinant HM2 was then produced in *Escherichia coli* cells following transformation with a synthetic gene.

Having characterised the hirudin gene from the Bangladesh population of *Hirudinaria manillensis* in another study (Scacheri *et al.* 1993), Scacheri compared the same gene in leeches from St Lucia with that from Bangladesh leeches. Working at the DNA level it was unnecessary to sequence the hirudin protein, thereby greatly reducing the number of leeches required. Furthermore, an important feature of this technical approach is the ability of isolating PCR-amplified clones from total RNA preparations extracted from very few leeches, sometimes even from one leech head. For the St Lucia population research focussed exclusively on the cDNA of the best characterised isoform of hirudin (HM1). By way of summary of these data, Scacheri found that the nucleotide sequence for the HM1 cDNA from the St Lucia population was identical to that from the Bangladesh population (Fig. 2). This applied also to the nucleotide sequence corresponding to the twenty amino acid signal peptide. In this context, it is very interesting to note in terms of the rate of evolution that, although the St Lucia and the Bengal populations have been isolated for approximately 150 years, the hirudin gene is very highly conserved.

In conclusion, based on comparative morphology, as well as on comparison of the nucleotide sequence of the hirudin gene, we hereby designate the leech described originally as *Hirudinaria* (*Poecilobdella*) *blanchardi* Moore, 1901 from Puerto Rico, and found also in St Lucia and Martinique, as the junior synonym of *Hirudinaria manillensis* (Lesson, 1842) of the Philippines and other parts of South-East Asia.

Systematics

Family Hirudinidae Whitman, 1886
Subfamily Hirudinariinae Sawyer, 1986
Genus *Hirudinaria* Whitman, 1886

Hirudinaria manillensis (Lesson, 1842)
(Figs 1A, 3)

? *Hirudo Martinicensis* Blainville, 1827: 250 (Martinique). (Not *Hirudo Martinicensis* Moquin-Tandon, 1826: 139).

Hirudo manillensis Lesson, 1842: 8 (Philippines, type material could not be located).

? *Hirudo Unicolor* Moquin-Tandon, 1846: 324 (new name for *Hirudo Martinicensis* preoccupied).

Limnatis (*Poecilobdella*) *granulosa* – Blanchard 1893: 28 (undissected); 1897: 345 (undissected).

Hirudinaria (*Poecilobdella*) *blanchardi* Moore, 1901: 214, pl. 12 (Puerto Rico, type material could not be located).

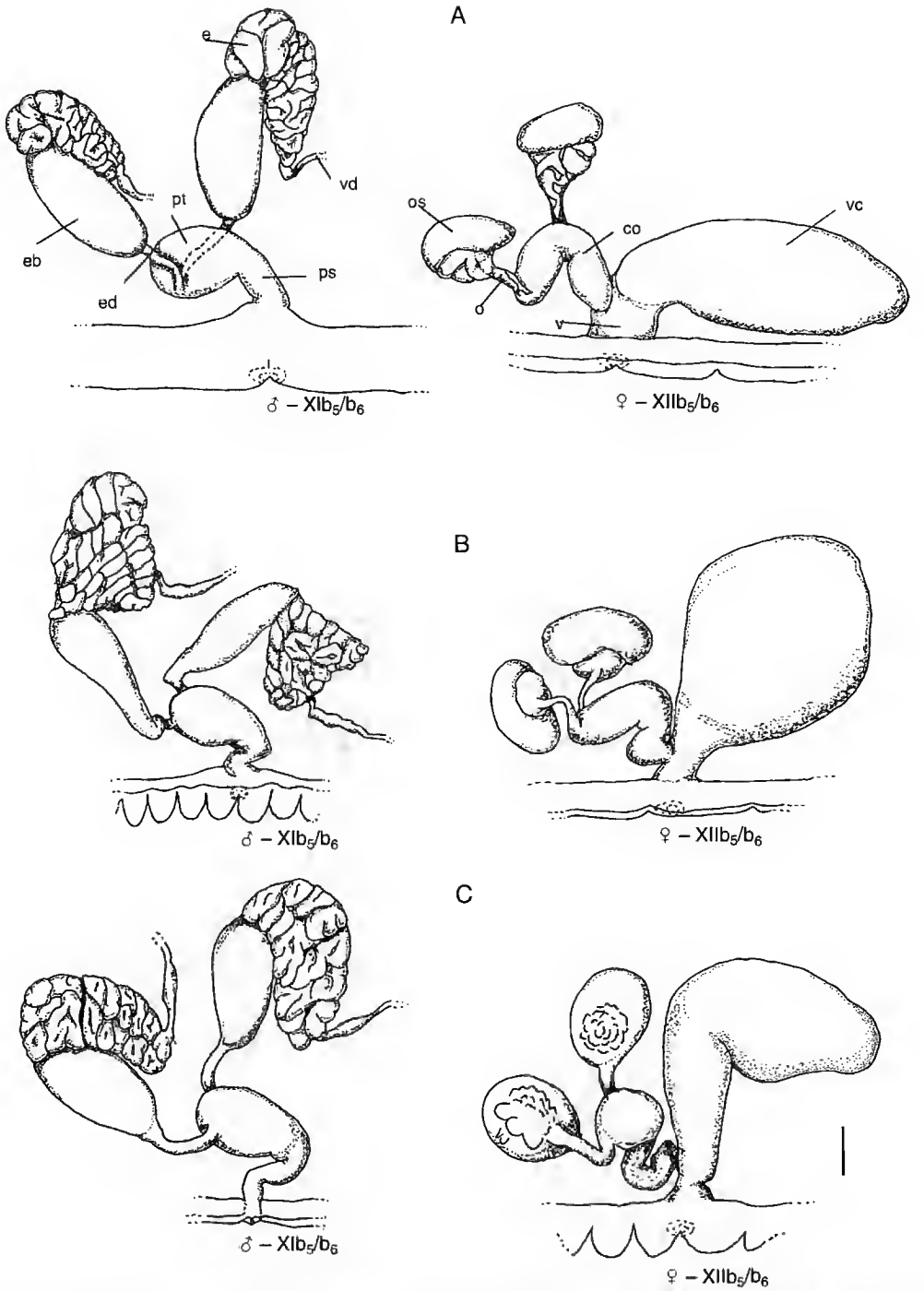

FIG. 3. — Comparison of taxonomically diagnostic features of the male (left) and female (right) reproductive systems of "buffalo" leeches collected from Asia and the West Indies. See "Methods" for specific localities. **A**, *Hirudinaria manillensis* from Luzon, Philippines (type locality); **B**, *Hirudinaria manillensis* from Bangladesh; **C**, *Hirudinaria manillensis* from Puerto Rico. Scale bar: 1 mm. See Fig. 1 for key to labelling and orientation.

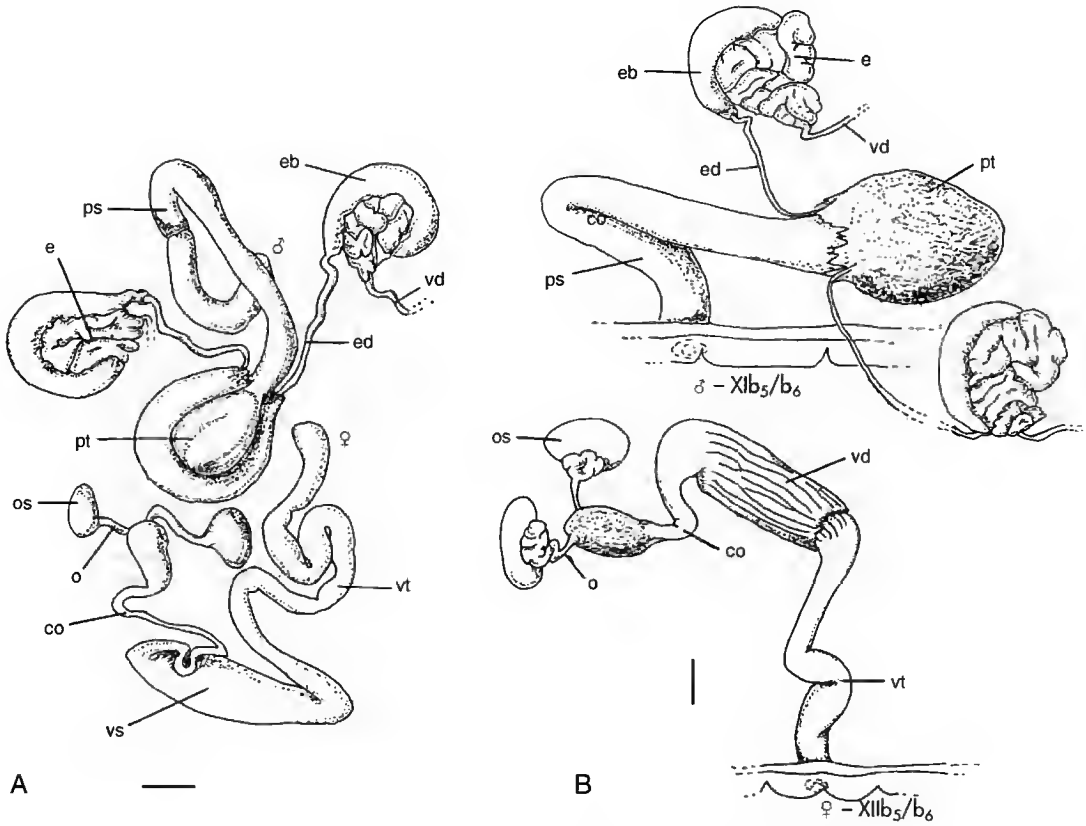

FIG. 4. — Comparison of taxonomically diagnostic features of the male (upper) and female (lower) reproductive systems of two species of the genus *Asiaticobdella*; **A**, *Asiaticobdella fenestrata* from Gambia, viewed from dorsal side, anterior to top; **B**, undetermined species of *Asiaticobdella* from Guadeloupe, viewed from the left side, anterior to left. See Discussion for specific localities. **vs**, vagina "*sensu stricto*"; **vt**, vaginal duct (or "stalk"). See Fig. 1 for key to other labelling. Scale bars: 1 mm. Note neither species has a vaginal caecum.

Limnatis granulosa – Oka 1934: 286, fig. (externals) (undissected).

Caribeobdella blanchardi – Ringuelet 1976: 13.

"*Poecilobdella*" *blanchardi* – Sawyer & Kinard 1980: 84 (Puerto Rico, dissected; Antigua and Haiti, undissected).

Hirudinaria manillensis – Sawyer 1986: 687, fig. 18.9E.

MATERIAL EXAMINED. — **Philippines.** Calumpang, Laguna, 14°10'N - 121°18'E, November 1986, collected by F. O. P. Hechtel.
Bangladesh. Sylhet, 24°53'N - 91°51'E.
Puerto Rico. SW Puerto Rico, Cartagena Lagoon, 27.VIII.1973, collected by J.W. Miller and I. Pomales, Department of Marine Sciences, U.P.R. Mayaguez, P.R. 00708.
St Lucia. Cattle pond 2/3 miles south of Micoud, 13°48.2'N - 60°55.8'W, September 1989, collected by R. T. Sawyer.
Martinique. Small stream, Tributary of Lazarde River, Route du Vert-Pré, Lamentin, 29.V.1998, collected by J. Vaubon.

Genus *Poecilobdella* Blanchard, 1893

Poecilobdella granulosa (Savigny, 1820)
(Fig. 1B)

Sanguisuga granulosa Savigny, 1820: 115 (type locality: Pondichéry, India).

Poecilobdella granulosa – Sawyer 1986: 687, fig. 17. 16B.

MATERIAL EXAMINED. — **India.** — Specimens supplied by a dealer in the "Madras area", 1984. — Specimens obtained in 1997 by Dr Ramesh Yadav from a Bombay dealer who reported they had been collected by the "Adivasi" people from the lakes near the city of Baroda, Gujarath State, India.

Subfamily HIRUDININAE Richardson, 1969
Genus *Asiaticobdella* Richardson, 1969

Asiaticobdella sp.
(Fig. 4B)

Hirudinaria blanchardi – Pointier, Théron & Imbert-Establet 1988: 38 (Guadeloupe, undissected).

MATERIAL EXAMINED. — **Guadeloupe.** Specimens purchased by R. T. Sawyer in the market at Pointe-à-Pitre, Guadeloupe, in August 1995. — Specimens collected alive on 6.II.1997 in little ponds to the north of the airport, west of Abmes, by N. Barré.

Asiaticobdella fenestrata (Moore, 1939)
(Fig. 4A)

Limnatis fenestrata Moore,1939: 343, pls 27, 28 (type locality: Botswana).

Asiaticobdella fenestrata – Sawyer 1986: 776, 777, fig. 18.14D.

MATERIAL EXAMINED.— **Gambia.** Live specimens acquired in July 1993 from a sacred crocodile pool at Katchikaeli (13°28'N - 16°40'W) in coastal Gambia, close to the southern bank of the Gambia River at its mouth, through the kindness of C. M. Moiser.

Researchers are cautioned that medicinal leeches in the West Indies cannot be distinguished from external characters alone and precise identifications must be based on dissection of the reproductive systems. To avoid confusion, researchers are advised to detail the nature of the reproductive system when making identifications, according to the following simplified key. It cannot be ruled out that more than one species of medicinal leech lives on any of the islands.

SIMPLIFIED KEY TO THE MEDICINAL LEECHES IN THE WEST INDIES

1. Vagina with a large caecum ("caecal pouch") (Fig. 1: vc) 2

— Vagina lacking a large caecum (Fig. 4B) ..... *Asiaticobdella* sp.
Known from Guadeloupe

2. Female reproductive system has a distinct "vagina" (elongate portion between the female gonopore and the common oviduct); male system lacking ejaculatory bulbs (Fig. 1B) ..... *Poecilobdella granulosa* (Savigny, 1820)
Not recorded from the West Indies

— Female reproductive system lacks an elongate "vagina"; male system with ejaculatory bulbs (Fig. 1A) ..... *Hirudinaria manillensis* (Lesson, 1842)
Known from Puerto Rico, Martinique and St Lucia

DISCUSSION

MECHANISM OF TRANSPORT OF LEECHES FROM INDIA TO THE CARIBBEAN

The leech on St Lucia, Martinique and Puerto Rico is actually the Asian medicinal leech *Hirudinaria manillensis* which appeared on the islands in the middle of the nineteenth century. To try to explain how the leech could have been introduced, we started looking for historic

connections, especially medical, between the West Indies and South-East Asia at about this time. We discovered a significant connection in the emigration of a large number of labourers from India into both the British and French islands (see Thomas 1985 for further background).

The economy of the West Indian colonies was largely built on sugar. This required heavy labour and African slaves were brought in for this purpose. In England the Emancipation Act of 1833 provided for the gradual freedom of the slaves in the colonies, this having been completed by 1838. To replace the slaves, the West Indian planters turned to India for immigrant labour. After some false starts amidst controversy with abolitionists, the Colonial Office in 1844 approved a scheme for indentured Indian emigration, wholly managed by the English government in order to protect the health and safety of the labourers. The emigrants were promised return passages to India after five years. In 1845 two shiploads of Indians reached British Guyana, and one ship each went to Jamaica and Trinidad. The voyage from Calcutta to Trinidad took between eighty-five and ninety-two days, typically stopping at Cape of Good Hope or St Helena. By further example, Captain J. H. Wilson, West India Emigration Agent, dispatched twelve ships in the 1845-1846 season and seventeen ships in 1846-1847, varying in passengers number from 203 to 423 (Public Record Office 1847: 158).

Because of a disruption following the Sugar Duties Act of 1846, large scale emigration from India was not again fully underway until 1851. In the 1850's the Windward Islands were allowed to recruit small numbers of Indian labourers on the usual terms, permission being granted to Grenada in 1856, St Lucia in 1858 and St Vincent in 1861. These small islands requested indentured labour only irregularly and in small numbers. For example, during the emigration period to St Lucia from 1859 to 1869, the English landed 4354 Indians from Calcutta.

The French emancipated their slaves in 1848 and an acute shortage of labour resulted in the colonies. The planters were very conscious of the example set by the English colonies (and the French island of La Réunion in the Indian Ocean). In 1852, an immigration law was passed providing officials to supervise recruiting and to look after the welfare of emigrants. Consequently the Compagnie Générale Trans-Atlantique arranged to supply 2000 or 3000 Indians each year. In 1854, an Immigration Committee was set up to control the whole operation. Subsequently, a full code of immigration regulations appeared as laws in 1855 and 1859 which made the rudimentary protective organization much more elaborate and efficient. The Compagnie Générale Maritime contracted to supply Martinique with 1500 Indians over four years.

The English government sought to persuade France to give up recruiting in Africa and in 1861 agreed to let the French colonies recruit labour in British India on much the same terms and under the same regulations as did the English colonies (Parliamentary Papers 1861). Some Indians had been brought in by the French in the 1850's, over 9500 into Martinique and perhaps 1000 into Guadeloupe from the French Indian territories of Pondichéry and Chandernagore. But these territories could supply only limited numbers, so British India became the recruiting ground. Altogether, between 1853 and the termination of the agreement with England in 1885, 25509 Indians were landed in Martinique, embarking mostly from Calcutta and Pondichéry. In Guadeloupe, until 1861, most of the migrants, mainly Tamil, originated from South India (mainly Pondichéry). From 1873 this stream became secondary compared with the Calcutta region (Centre d'Études 1982). From 1856 to 1889 over 40000 Indians landed in Guadeloupe.

In order to ensure the health of the emigrants, Her Majesty's Colonial Land and Emigration Commissioners enforced strict conditions and medical requirements onto the contractor of each shipload of emigrants (Public Record Office 1847). As shown below, each ship from India taking emigrants to the West Indies from the mid-1840's to the early 1870's was required to have leeches on board for medicinal purposes. Based on the following historical evidence, we propose this was the most probable mechanism by which *Hirudinaria manillensis* came to be in St Lucia and other islands of the West Indies.

From British India: Calcutta and Madras

The records of the Public Record Office (PRO) and the Oriental and India Office in London include the following observations, relevant to our study. For administrative reasons, the British ships transporting Indian emigrants to the West Indies embarked almost exclusively from either Calcutta or Madras (Public Record Office 1847). In order to ensure the health of the emigrants, Her Majesty's Colonial and Emigration Commissioners enforced strict conditions and medical requirements on the contractors (Public Record Office 1847). Each ship was required to have a list of medical supplies before embarkation. In 1847, this "List of Medicines and Medical Comforts" included one hundred leeches for up to 100 emigrants, to be increased by 50 for each 100 emigrants beyond 100 (Public Record Office 1847: 21). From the example of Captain J. H. Wilson given above, his twelve ships would have transported toward the West Indies a total of approximately 2 000 Indian leeches in the 1845-1846 season, and similarly his seventeen ships would have carried approximately 3000 leeches in the 1846-1847 season. Interestingly, these particular ships originated from Madras and were bound for British Guyana, Trinidad and Jamaica, none of which appears to harbour the leech today.

The leeches had to originate "fresh" at the port of embarkation of Calcutta or Madras and "not England". In a letter dated 10 March 1847 to the West India Emigration Office, Madras, the same Captain J. H. Wilson recommended "that a clause be introduced in the Charter strictly enjoining that vessels shall purchase every article of provision required by the regulations fresh at the port of embarkation" (Public Record Office 1847: 337). Similarly, in the Emigration Commissioners' official "Tender for the Conveyance of Indian Emigrants to the West Indies" dated June 1847, item eight records "[...] and also a supply of Medicine and Medical Comforts according to the annex [...]. Provided always, that all articles of Provisions for the use of the Emigrants shall be provided and put on Board in India and not in England" (Public Record Office 1847: 21). In other words the leech species in question originated in British India, *i.e. Hirudinaria* and therefore certainly would not have been the European medicinal leech *Hirudo medicinalis* which does not live in the Indian subcontinent (Sawyer 1986: 571).

Records show that medicinal leeches were required to be on board emigrant ships from 1847 to 1871. In the 1856 "Rules for Regulating all Matters Connected with Emigration from Madras to the West Indies" 500 leeches were required for 50-100 emigrants (India Office 1856: 17). The 1859 "Revised Rules Re Coolie Emigration Including a List of Medicines" required 50 leeches per 100 persons; 75 per 200 persons; 100 per 300 persons; and 100 per 350 persons (Public Record Office 1859: 36). The 1864 "Rules for the Guidance of the Protector of Emigrants in Calcutta" required 50 leeches per 100 persons; 75 per 200 persons; 100 per 300 persons; and 100 per 350 persons (India Office 1864: 4). The 1871 "Emigration from the Port of Madras. Rules under Act of 1871" required 50 leeches per 100 persons; 75 per 200 persons; 100 per 300 persons; and 125 per 400 persons (India Office 1874). In the same year the 1871 schedule 3 "The Medicines, Rules Under Act VII (The India Emigration Act)" required "leeches" but no numbers were specified (India Office 1872: 394). Interestingly, the 1883 "Rules Relating to Emigration from Calcutta" required "one sixteen oz blood portinger" but no mention of leeches (India Office 1884). We have not found any record of the actual medical use of leeches on board these emigrant ships, but such records are to be expected since each ship's surgeon was required to keep a medical diary.

A few records document that leeches were used medicinally in the Caribbean region about this time. Leeches were used successfully following arterial surgery in the Hospital of St Felipe and Santiago, Havana, in 1849 (Wills 1849: 148, 149). Dr Hector Gavin MD FRCS, Lecturer on Forensic Medicine at Charing Cross Hospital, London, in his 1851 report regarding a recent outbreak of Yellow Fever in Surinam, enclosed a translation of a report by the Dutch Medical Officer H. Schomnberg of 5 September 1851 on the treatment of Yellow Fever near Paramaribo, Surinam. Leeches were part of the treatment: "leeches [...] generally proved very

beneficial [...]" and "[...] Leeches produced a very satisfactory result" (Public Record Office 1851).

In France and England, the use of leeches reached a peak about 1820-1845 and gradually fell out of favour by the 1870's (Sawyer 1981). Bloodletting, but not necessarily leeching, continued on British ships up to the 1880's and 1890's and probably later, but the practice was becoming suspect. For example, Acting Assistant Surgeon M. Elphington Greany of HMS *Vestral* in 1869-1870 recorded the following: "[...] Dr. Bellot, a great Havana authority on Yellow Fever, is accustomed, I understand, to bleed in almost all cases, if seen in the early stage, and I myself have been advised in Port-au-Prince to use the lancet, but I saw no case in which it would be allowable to do so. I should rather fancy that such a proceeding would be fatal to any chance of a patient's recovery" (Public Record Office 1870).

Although we have documented that thousands of Indian medicinal leeches *Hirudinaria* were transported to the West Indies from the mid-1840's to the early 1870's, the final fate of these leeches is so far undocumented. We are aware that: "Ship's surgeon shall receive charge of medical stores. He must ascertain quality and that the supplies are not short. On arrival at the port of debarkation the surgeon is to deliver the balance of medical stores to the Emigration Agent at that port with a statement of issues during the voyage" (India Office 1864: 4). We propose that some of the *Hirudinaria manillensis* ended up in local water and established themselves.

From French India: Pondichéry

Apart from the account above of labourers going to Martinique and Guadeloupe from Pondichéry, and later from Calcutta in cooperation with the English emigration policy, we have not found direct evidence that leeches were put on board in Pondichéry for ships destined to the West Indies. Moquin-Tandon (1846: 341) did record that a medicinal leech, which he called "*Hirudo granulosa*" was "employed by the doctors of Pondichéry". In an 1857 report from the India Board to the British Colonial Office regarding Indian emigration on board British ships from Pondichéry to French colonies in the West Indies, a list of required medicaments did not specify leeches (Public Record Office 1857: 318). However, Leuckart and Brandes claimed, unfortunately without giving any further detail, that *Hirudinaria* at one time "was shipped out of India (Pondichéry) in large quantities to the islands of Bourbon and Mauritius" in the Indian Ocean (Leuckart & Brandes 1901: 879). Interestingly, under the Convention with the French, the British in 1862 transported over 4500 Indians into La Réunion from Calcutta and Pondichéry (Public Record Office 1862).

Leech Importation into Mauritius

The economic and social history of Mauritius in the southern Indian Ocean is remarkably similar to that of islands of the French West Indies. In 1997 Sawyer visited Mauritius to determine whether medicinal leeches had been imported into the island in the past and whether the leech may have escaped, as in the West Indies (Sawyer in press). By searching through advertisements in the colonial newspaper *Le Cernéen, Journal de l'Île Maurice*, clear evidence was found that for at least the forty year period from 1833 to 1872, large numbers of leeches were intentionally imported from Pondichéry into Mauritius by local pharmacists for medicinal purposes (Fig. 5). A selection of such advertisements follows:

31 mai 1833. "Chez M. Grosjeau neveu, rue St George : belles sangsues de l'Inde arrivées par l'*Antoinette*."
Note: on 11 June 1833 "Arrivages [...] La barque l'*Antoinette*, capit. Colin, partie de Madras, et de Pondichéry le 15 avril ; cargaison riz et diverses marchandises. Passagers vingt Indiens."

2 mars 1848. "Belles Sangsues de Pondichéry, à 1 p. la douzaine. S'adresser à M. Guior ou à M. E. Fleurot."
Note: previously recorded ships from Pondichéry, reported on 22 February 1848: (a) Brig. "*Mauritius Packet*" from Pondichéry, 12 January, "with sundries for this port"; and (b) Bark "*East Anglian*" from Pondichéry, 18 January, "with sundries for this port".

25 avril 1872. "Belles Sangsues de Pondichéry s'adresser à la Pharmacie B. Perrot, rue Desforges, n° 67."
Note: this street now is Sir Seewoosagur Ramgoolan St, Port Louis.

A VENDRE.

Véritable vin de Constance blanc et rouge en chopines, bon porter en bouteilles à 2 p. 75 c. la douzaine.

S'adresser à M. D. Bonnefin, jeune, rue St-Georges.

— *Chez M. BENOIT, marchand, rue Desforges : bière d'Hugdson, première qualité, à 2 p. 25 c. la douzaine et 40 s. la bouteille ; vin de Bordeaux, première qualité, à 25 s. la bouteille ; bougie diaphane d'Angleterre ;* le tout au comptant.

— *En gros ou en détail, BELLES SANGSUES, arrivées de Pondichéry par le navire* l'Emmée.

S'adresser au magasin Heynemans.

Belles SANGSUES

DE PONDICHÉRY.

S'adresser à la Pharmacie B. PERROT, rue Desforges, No. 67.

FIG. 5. — Representative advertisements by pharmacists in Port Louis, Mauritius, in the colonial newspaper *Le Cerneen, Journal de L'île Maurice*. Top: 6 December 1833. Bottom: 25 April 1872. Leeches sold in pharmacies in Mauritius in the southern Indian Ocean were imported from Pondichéry, India, for over forty years.

No evidence was found that some of the ships carrying leeches from Pondichéry went on to the French West Indies to supply medical demand, but that possibility must be left open. Unfortunately, the species of leech imported into Mauritius from Pondichéry in the nineteenth century remains as yet undetermined

Although many medicinal leeches were indeed imported into Mauritius, there is no evidence that the leech species in question escaped and established itself in the wild. Quite the contrary while several leech species were collected on the island, no bloodsucking species at all were encountered (Sawyer 1997, personal observation). Local people very familiar with the wildlife of Mauritius were unanimous in confirming that no bloodsucking leeches occur on the island today.

MEDICAL ETHNOLOGY

Leeches were enormously valued for medical purposes in the last century and practitioners were highly motivated to acquire them. Since the medical need for leeches undoubtedly motivated their importation into the Caribbean area in some numbers, an ethnological assessment of the current medical use of leeches in this region is relevant to this study. Sawyer carried out numerous interviews of local people on various West Indian islands, as well as French Guyana, Surinam and Mauritius. Of much value were the local markets where leeches were still being sold in recent times. Whenever possible such market leeches were purchased for later identification. A more formal medical ethnological study was undertaken in rural St Lucia, where in-depth interviews were conducted by Sawyer with six local people recognized as "healers" by the St Lucia National Trust. The latter study was carried out in French patois in September 1989 with the invaluable assistance of Mr. Laurent

Jean Pierre of the St Lucia National Trust, Castries. Historical evidence presented above suggested that the St Lucia leech may have originated from Bengal, where it had been used medicinally in the last century. To learn more Sawyer went to Dhaka, Bangladesh in July 1992, where he conducted extensive interviews with local street vendors who were still selling *Hirudinaria manillensis* for medicinal purposes in time immemorial tradition.

Locally collected leeches were still being sold for medicinal purposes on some of the islands of the West Indies, including the main markets in Castries, St Lucia (1989), Fort-de-France, Martinique (1993, but not by 1998) and Pointe-à-Pitre, Guadeloupe (1995). As late as 1976 medicinal leeches were being sold in at least one pharmacy in Cayenne, French Guyana, but by 1993 no pharmacist contacted in Cayenne was aware of anyone using leeches anymore in French Guyana (Sawyer personal observation).

In St Lucia (1989) much effort was made to interview market sellers, local practitioners and recipient users of leeches in urban as well as in remote regions. Today, these are almost exclusively people of African descent who speak French patois as their first or only language, even on this nominally "British" island. In the Castries market more than one vendor sold leeches ("sansi" corrupted from the french "sangsues"). Leeches, reportedly from Dennery, were purchased from one vendor and later identified definitely as *Hirudinaria manillensis*. The market leeches were in any sort of bottle, which invariably had a piece of charcoal at the bottom. One seller explained (erroneously) the leeches "ate the charcoal" which could be "dried and re-used". Most people seemed to be aware of leeches and their medicinal use, and usually knew a relative who had used them some time in the past. Several people made the comment that leeches were less commonly used now than a couple of generations ago. One young man said his grandmother "used to keep them around her house". Leeches were used sparingly, but for appropriate conditions, such as for "black eyes", "swollen feet", "boils", "blood poisoning" and "snake bite". Some were applied "to the back" for undiagnosed conditions, and one young woman's grandfather reportedly had leeches applied several times a week for a while for some undiagnosed conditions. Leeches apparently were not used for eye complaints except black eyes. They could be re-used by placing salt on them and squeezing out the blood. One intelligent old man recognised as a local "healer" volunteered that his grandmother told him that ethnic Indian people (*i.e.* from India) were "the best users of leeches". This same observation was made by a French scientist in St Lucia in reference to Guadeloupe. Several people observed that leeches were less abundant now than when they were young. They attributed this decline to the "pesticide being used to treat nematodes", and to "banana irrigation". It was reported several times that more than one species of leech lives in St Lucia ("one does not bite" by one account, and "one very aggressive but not so good; the slow sticking one better" by another account). Sawyer could not confirm a second hirudinid species in St Lucia from his limited field studies there. One well-traveled St Lucian observed that leeches were more abundant in St Lucia than in any of the other islands. Sawyer can certainly confirm that leeches, identified as *Hirudinaria manillensis*, were locally very common in St Lucia in September 1989. (Sawyer was reliably informed, but has not yet confirmed, that leeches occur and are also used medicinally on Dominica and Granada).

Most of the West Indies today is populated mainly by people of African descent, and many aspects of the culture reflect this African heritage. In a separate on-going study, Sawyer has found no evidence that live leeches were ever used in traditional medicine in black Africa. At the same time, it is well-documented that bloodletting and cupping were, and continue to be, widely practiced there (*e.g.* Livingstone 1857: 129, 130). In contrast, the medicinal use of leeches was commonplace to French and British colonists, as well as widely practiced by people of the Indian subcontinent. The so-called "buffalo" or "cattle" leeches have been used medicinally for over two thousand years in the Indian subcontinent, a practice which continues today. On the streets of Dhaka, Bangladesh, the species used is *Hirudinaria manillensis* (Sawyer 1992, personal observation). Leeches are still commonly used in

the traditional (Ayurvedic) hospitals and clinics of Bombay on the west coast of India. Some specimens of the leech used clinically in Bombay were sent to Hechtel for identification by Dr Ramesh Yadav and were found to be *Poecilobdella granulosa*. Leeches of an undetermined species are reportedly still being used in the villages in the hinterland of Sri Lanka (Sawyer 1995, personal observation).

The use of these large, aggressive leeches is described in considerable detail in Chapter XIII of the *Susruta Samita* which records the ancient Ayurvedic form of Indian medicine (Bhishagratna 1963: 98-105), dating back by some accounts to 200 BC. One would expect these people to bring this tradition with them to the West Indies, bearing in mind that the Europeans had already been using leeches there.

A case of recent leech colonisation

The ability of a medicinal leech species to colonize an isolated pond very rapidly has been thoroughly documented during a fifteen year study from 1972 to 1987 in a small lake in Guadeloupe (Pointier *et al.* 1988). Lake Grand Étang is located in the rain forest at an altitude of 450 m and has "no permanent human habitation within a radius of 3 km". During a biological survey in 1972, there were no leeches in the lake, but in 1973 a locally common species of leech was introduced by local people. The leech population increased rapidly where they fed mainly on the tilapid fish *Oreochromis mossambicus* (Peters, 1844). The leeches became "an important new factor contributing to fish mortality; many dying fish were seen floating on the lake or stranded in the aquatic vegetation". This well-documented case may give us a clue to the success of this and possibly other leech species, *i.e.* their ability to thrive on the fish *O. mossambicus* which was introduced to the West Indies from Africa as a source of protein. (Note: this leech species which understandably was called *Hirudinaria blanchardi* is probably the same as the Guadeloupe "market leech" discussed below).

Evidence for a second introduced leech in the West Indies: Guadeloupe market leech

Until recently, we had presumed in our investigation that all medicinal leeches found on the various islands of the West Indies represented a single species, *Hirudinaria manillensis*, which we had concluded came from India in the mid-1800's. Most of our morphological and molecular genetics data were based on specimens collected alive in St Lucia, and corroborated with morphological data from specimens collected alive in Puerto Rico and Martinique. The first hint that a second medicinal leech species is present in the West Indies resulted from dissecting specimens purchased by Sawyer in the market at Pointe-à-Pitre, Guadeloupe, in August 1995. To our surprise this "market leech", while looking similar externally to *Hirudinaria manillensis*, is quite different internally. The jaw structure and reproductive organs clearly demarcate it from all other hirudinid species (Macrobdellinae) of the New World. (To confirm that the "market leech" actually lives in the wild in Guadeloupe rather than purchased from outside the island, N. Barré kindly collected live specimens of the same leech species west of Abymes. Hechtel confirmed by dissection that these were the same as the "market" species).

Though in appearance very similar to *H. manillensis*, dissection of the reproductive systems of the Guadeloupe "market leech" (Fig. 4B) revealed it to be an undetermined species of the genus *Asiaticobdella*. This genus belongs to the Hirudininae, a subfamily distinguished from the Hirudinariinae by the absence of a spacious vaginal caecum. As currently defined (Sawyer 1986: 688), the genus *Asiaticobdella* occurs in both India and Africa (Harding & Moore 1927). Although the authors are unable to rule out an *Asiaticobdella* of Indian origin, historic and taxonomic evidence presented below leaves open the possibility that the Guadeloupe leech may be of African origin.

After failing in the last century to introduce the European medicinal leech *Hirudo medicinalis* into the French West Indies, M. Gerbidon, interim governor of Senegal, proposed in 1827 the idea of sending leeches from Senegambia on the north-west coast of Africa (*e.g.* Dupuy 1830; Calve 1830) to the Antilles, including to Cayenne, French Guyana. After at least one failed attempt, in June 1829, he successfully ship-

ped 50 000 leeches from Senegal, of which 34 000 survived. Of these the French authorities purposely released about 16 000 into the ponds and streams of Guadeloupe. In December 1829 it is recorded that "the Negroes have found them on their legs and on the legs of animals, and fishermen have seen several in their nets (nasses). Unfortunately, Negroes have sold a great number of them in Pointe-à-Pitre."

In order to elucidate the possibility that leeches may have been introduced from Senegambia, Hechtel acquired live specimens of a candidate hirudinid leech from coastal Gambia. After careful study of its external and internal characters (Fig. 4A) Hechtel confidently identified this Gambian leech as *Asiaticobdella fenestrata* (see Sawyer 1986: 774-778 for key to African Hirudiniformes). This study also confirmed that the Gambian leech was not the same as the Guadeloupe leech. They differ specifically in that *A. fenestrata* has a vaginal duct about 2.5 to 3 times the length of the vagina (*sensu stricto*) whilst the Guadeloupe leech has a vaginal duct about 1.5 times the length of the vagina. The penis sheath is also commensurately longer in *A. fenestrata*. To date we have not been able to match the Guadeloupe leech with any descriptions or specimens known to us. However, some very old specimens labelled "*Mare d'Issy, Sénégal, Bocall A811*" were obtained from the Muséum national d'Histoire naturelle. Unfortunately, they were too brittle for a definitive identification but the relative shortness of the vaginal duct distinguished them from *A. fenestrata* and leaves open the speculative possibility they are the same as the Guadeloupe "market leech".

The exact species of leech introduced from Senegambia in the 1820's is so far unclear from historic records. In fact, Virey (1829) records that "Senegal has several hirudinid species in its ponds, lakes and streams". One candidate, however, which should be eliminated, is a virtually unknown species described by Henry, Sérullas and Virey in 1829 as *Sanguisuga mysomelas* from "Senegal, particularly in lakes Mboroo and Nghier" (Virey 1829; Moquin-Tandon 1846: 14, 340), but apparently it has not been recorded since. Interestingly, it was noted about this species that doctors at the time "must always use double those of Europe for the same amount of blood drawn" (Virey 1829).

Erratic distribution of medicinal leeches on West Indian Islands

One of the inexplicable findings concerning medicinal leeches in the West Indies is their erratic distribution, being prolific on some islands but totally absent on others. For example, such leeches are known to occur on Martinique, Guadeloupe (Pointier *et al.* 1988), Dominica, St Lucia, Haiti, Antigua (Sawyer & Kinard 1980), and Puerto Rico (Moore 1901; Sawyer & Kinard 1980). At the same time, it appears to be absent from Jamaica, Barbados, St Maarten/St Martin, Surinam and French Guyana, as well as from Guyana, Trinidad, Bahamas and probably Cuba. It is still unclear whether the reason(s) for this unusual distribution are historical or ecological, or both.

It is almost certain that leeches have been shipped freely between islands for medicinal purposes for the past 150 years, a practice that is still going on. During periodic visits to the West Indies region from 1974 to 1998, Sawyer obtained credible oral evidence that in recent times leeches are still being shipped for medicinal purposes to certain leech-free islands, as well as to the mainland of South America. For example, local residents claim that a leech is still imported from time to time into St Martin/St Maarten from "another island", and into Trinidad reportedly from "Granada". As late as 1976, leeches were being shipped regularly from Martinique, reportedly "from the ponds near the airport", to Cayenne, French Guyana, but by 1993 no leeches were apparently being imported into French Guyana (Sawyer 1993, personal observation).

Acknowledgements

This study began over twenty-five years ago in 1974 during a trip by R. T. Sawyer to Puerto Rico where he first encountered and was perplexed by a large aggressive leech unlike any other in the New World. It took many years to prove, to our satisfaction, the true identity of the leech and to determine when and by what mechanism it had arrived in the West Indies.

Along the way many people contributed to pieces of the puzzle. We especially thank N. Barré of the Département d'élevage et de médecine vétérinaire CIRAD-EMVT, Pointe-à-Pitre, Guadeloupe, and C. M. Moiser, Plymouth College of Further Education, England for collecting live specimens of leeches from Guadeloupe and Gambia, respectively; and to Prof. J.-L. Justine, Laboratoire de Biologie Parasitaire, Protistologie, Helminthologie, Muséum national d'Histoire naturelle, Paris, for furnishing preserved specimens from Guadeloupe and Senegal. In Martinique, R. T. Sawyer is particularly grateful to M.-J. Lamorandière, Sofitel Bakoua, Les Trois Îlets, and to M. Tanasi, Office National des Forêts, Fort-de-France for exceptional assistance in obtaining specimens of the Martinique leech in the "dry" season. We are also very grateful to W. F. Kinard, University of Charleston; R. Munro, Swansea, Wales; J. P. Pointier, Centre de Biologie et d'Écologie Tropicale et Méditerranéenne, Perpignan, France; M. Théry, Laboratoire d'Écologie générale, CNRS; R. K. Yadav, Central Council of Indian Medicine, Bombay; and to Mrs E. F. Thomson, Richmond, England. For invaluable assistance in Mauritius, R. T. Sawyer would like to thank the following: P. Sooprayen, Chief Archivist; R. Gopaul, Ministry of Health; C. Michel and Y. Martial.

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New Pisaniinae (Mollusca, Gastropoda, Buccinidae) from New Caledonia, with remarks on *Cantharus* and related genera

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ABSTRACT

The genera *Cantharus* Röding, 1798, *Pollia* Gray *in* Sowerby, 1834, and *Cancellopollia* n.g. (type species: *C. gracilis* n.sp.), are pisaniine buccinids having a small tooth (labral spine) at the edge of the crenulated outer lip. As defined and restricted here, these genera have a mainly Indo-West Pacific distribution. *Cantharus septemcostatus* n.sp., *Pollia pellita* n.sp., *Cancellopollia gracilis* n.sp., and *C. ustulata* n.sp., are reported from deep water in the New Caledonia region, and *Cantharus leucotaeniatus* Kosuge, 1985 and *Pollia vicdani* (Kosuge, 1984) n.comb. are reported from Vanuatu. Despite a narrow bathymetric (415-560 m) and horizontal (northernmost Norfolk Ridge) distribution, *Cancellopollia gracilis* exhibits remarkable variation, with highly localised morphs.

KEY WORDS
New Caledonia,
bathyal,
seamount,
Buccinidae,
new taxa.

RÉSUMÉ

Pisaniinae (Mollusca, Gastropoda, Buccinidae) nouveaux de Nouvelle-Calédonie et remarques sur Cantharus *et genres apparentés.* Les genres *Cantharus* Röding, 1798, *Pollia* Gray *in* Sowerby, 1834, et *Cancellopollia* n.g. (espèce-type : *C. gracilis* n.sp.) sont des Buccinidae Pisaniinae caractérisés par la présence d'un petit denticule (épine labrale) faisant saillie au milieu des crénulations de la lèvre externe. Tels qu'ils sont redéfinis et restreints ici, sur la base de leurs espèces-types, ces genres ont essentiellement une distribution Indo-ouest Pacifique. Les espèces *Cantharus septemcostatus* n.sp., *Pollia pellita* n.sp., *Cancellopollia gracilis* n.sp. et *C. ustulata* n.sp. sont signalées des pentes bathyales de la région néo-calédonienne, et *Cantharus leucotaeniatus* Kosuge, 1985 et *Pollia vicdani* (Kosuge, 1984) n.comb. sont cités du Vanuatu. On ne connait aucun signalement du genre *Cantharus* à l'est des îles Fidji, où il est présent dans le Pléistocène, mais n'est pas connu dans l'Actuel. Malgré sa répartition limitée à une étroite bande bathymétrique (415-560 m) dans l'extrême nord de la Ride de Norfolk, *Cancellopollia gracilis* présente une variation remarquable, avec des formes morphologiquement reconnaissables très étroitement localisées sur des monts sous-marins isolés.

MOTS CLÉS
Nouvelle-Calédonie, bathyal, mont sous-marin, Buccinidae, nouveau taxon.

INTRODUCTION

The Pisaniinae comprises a large subfamily of mainly tropical carnivorous buccinid neogastropods. Although Cernohorsky (1971, 1975) provided an extensive review of Indo-West Pacific species, the generic classification of the Pisaniinae requires revision, and several deep-water taxa remain to be described. In the very extensive material collected by the MUSORSTOM expeditions to New Caledonia and nearby regions, several hitherto undescribed species related to the genera *Cantharus* and *Pollia* have come to light. Our purpose here is to describe these species, to propose the new genus *Cancellopollia* for two of them, and briefly to comment on the limits and distinguishing features of *Cantharus* and *Pollia*.

The names *Cantharus* Röding, 1798 (type species: *Buccinum tranquebaricum* Gmelin, 1791), *Pollia* Gray *in* Sowerby 1834 (type species: *Buccinum undosum* Linnaeus, 1758), and *Tritonidea* Swainson, 1840 (type species: *Buccinum undosum* Linnaeus, 1758; thus an objective synonym of *Pollia*) have been applied to a diverse array of Paleogene to Recent gastropods with ovate to fusiform shells, a convex crenulated outer lip, and sculpture consisting of strong spiral cords crossing strong to obsolete axial ribs or folds (see, *e.g.*, Bellardi 1872; Cossmann 1901; Peyrot 1927; Wenz 1941; Glibert 1963; Cernohorsky 1971, 1975). This broad and inconsistent usage stems from the failure of most earlier authors to take inro account important shell chatacters that can serve to distinguish a number of distinct clades. Although we do not wish to attempt a complete generic revision here, we take the opportunity to redefine *Cantharus* and *Pollia* in order to place the new genus *Cancellopollia* in the proper context.

We restrict the genus *Cantharus* to pisaniine buccinids with the following characters: shell ovate; teleoconch consisting of six or more shouldered whorls separated by a deeply impressed suture; base of last whorl constricted above short siphonal canal; sculpture consisting of strong, widely separated axial folds, strongest on adapical part of whorls and fading below, crossed by strong spiral cords and threads of various sizes; siphonal fasciole prominent, sculptured with fine spiral threads, demarcating a narrow umbilical slit that in many species is closed; outer lip weakly convex in profile, crenulated at edge; fourth or fifth crenulation from abapical end of outer lip enlarged to form blunt labral tooth or spine, formed in adult shell at termination of external groove; external terminal varix absent; inner side

of outer lip lirate, the number of lirae corresponding with the number of external spiral cords; columella smooth; inner lip adherent or weakly erect on abapical two-thirds, marked by a few ridges on adapical sector and by a weak parietal rib at its adapical end; parietal rib flanked on outer lip by one or two slightly enlarged tooth-like lirae; adapical end of aperture broad.

As restricted here, the genus *Cantharus* is exclusively Indo-West Pacific in distribution. It occurs along continental margins and adjacent to high islands. Living species are known from the Indian Ocean east to the Philippines, northeastern Australia, New Caledonia and Vanuatu (see below). During the Pliocene and Pleistocene, the genus was also represented in Okinawa and Fiji (see below).

The genus *Pollia* differs from the closely related *Cantharus* by having a more fusiform shell, adapically more tapered and narrower aperture, and a stronger parietal rib; by the presence of an external terminal adult varix; and by having a very small labral tooth located midway along the edge of the outer lip instead of on its abapical one-third. The labral tooth is absent on many individuals of the type species, *P. undosa*, which also differs from other species of *Pollia* by having obsolete axial folds. Most species of *Pollia* occur in the Indo-West Pacific. The very widely distributed *P. fumosa* (Dillwyn, 1817), however, extends east to the Galapagos Islands; and *P. vermeuleni* (Knudsen, 1980) is a West African species.

Most other species that have been assigned to *Cantharus* and *Pollia* (or its synonym *Tritonidea*) lack a labral tooth or, in the case of some tropical eastern Pacific species of *Muricantharus* Olsson, 1971 (type species: *Pseudoneptunea panamica* Hertlein *et* Strong, 1951), have a small labral tooth formed as an extension of a spiral cord. Although Cernohorsky (1975) synonymized *Muricantharus* and other taxa from tropical America and the eastern Atlantic with *Cantharus*, species from these regions belong to genera other than *Cantharus* and *Pollia*. Similarly, none of the many species assigned to *Cantharus* and *Pollia* (or *Tritonidea*) from Cenozoic strata in Europe, West Africa, or the Americas belongs to *Cantharus* or *Pollia*.

ABBREVIATIONS

AMS	Australian Museum, Sydney
MNHN	Muséum national d'Histoire naturelle, Paris
NM	Natal Museum, Pietermaritzburg
NMNZ	Museum of New Zealand *Te Papa Tongarewa*, Wellington
dd	dead specimen
lv	live specimen

SYSTEMATICS

Class GASTROPODA
Superfamily BUCCINOIDEA Rafinesque, 1815
Family BUCCINIDAE Rafinesque, 1815
Subfamily PISANIINAE Gray, 1857
Genus *Cantharus* Röding, 1798

Cantharus septemcostatus n.sp.
(Figs 1A, 2A, 3A, 7A)

TYPE MATERIAL. — Holotype in MNHN; paratypes: 2 (MNHN), 1 (AMS), 1 (NMNZ), 1 (NM).

TYPE LOCALITY. — North of New Caledonia, 19°05'S, 163°22'E, 220-225 m (R.V. *Alis*, SMIB 6, stn DW129).

ETYMOLOGY. — Latin *septem*, seven, and *costatus*, ribbed, with reference to the axial sculpture.

MATERIAL EXAMINED. — **North of New Caledonia**. MUSORSTOM 4, stn CP152, 19°06'S, 163°22'E, 223 m, 1 dd. — Stn CP189, 19°07'S, 163°29'E, 210 m, 1 juv. dd.
LAGON, stn 1147, 19°08'S, 163°30'E, 210 m, 2 dd. — Stn 1148, 19°07'S, 163°30'E, 220 m, 1 lv (paratype MNHN).
SMIB 6, stn DW108, 19°07'S, 163°30'E, 210-220 m, 1 dd. — Stn DW110, 19°05'S, 163°30'E, 225-230 m, 1 lv, 1 dd. — Stn DW113, 19°03'S, 163°30'E, 250 m, 1 lv (paratype MNHN). — Stn DW127, 19°07'S, 163°23'E, 190-205 m, 1 dd. — Stn DW128, 19°06'S, 163°22'E, 205-215 m, 2 dd. — Stn DW129, 19°05'S, 163°22'E, 220-225 m, 3 lv (paratypes AMS, NMNZ), 4 dd (holotype, paratype NM). — Stn DW130, 19°05'S, 163°21'E, 225-230 m, 1 lv, 3 dd.
BATHUS 4, stn DW934, 19°05'S, 163°29'E, 231-240 m, 2 lv, 1 dd.

DISTRIBUTION. — North of New Caledonia, alive in 220-250 m.

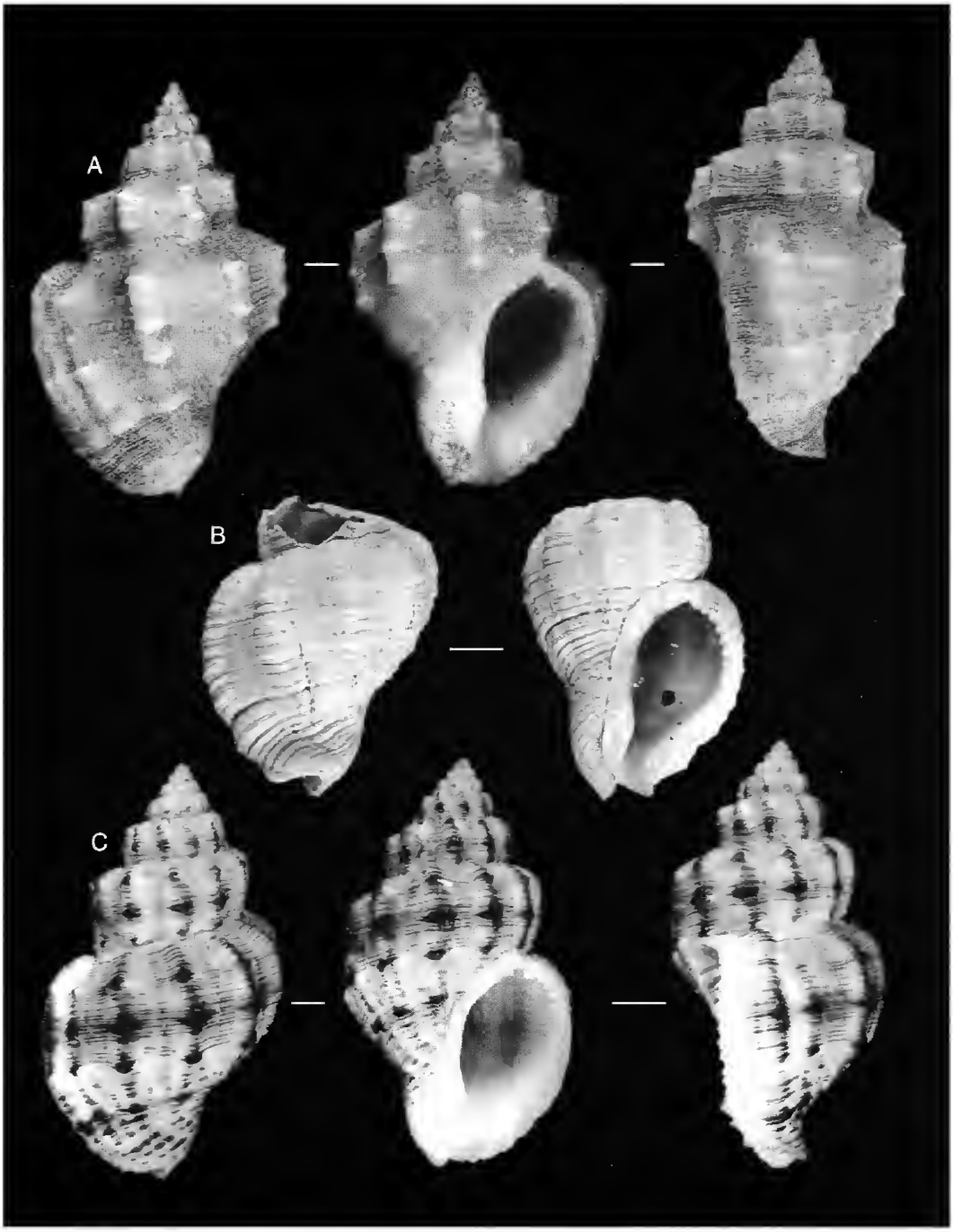

FIG. 1. — *Cantharus*; **A**, *C. septemcostatus* n.sp., north of New Caledonia, holotype, 36.2 mm; **B**, *C.* sp., Nakasi Beds, Early Pleistocene (1.8 Ma); Saunitambu, 18°02'S, 178°29'E, Viti Levu, Fiji, Kohn coll. 1982, 28 mm; **C**, *C. leucotaeniatus* Kosuge, 1985, Pta Engano, Cebu, Philippines, leg. Kosuge (MNHN), 47.5 mm.

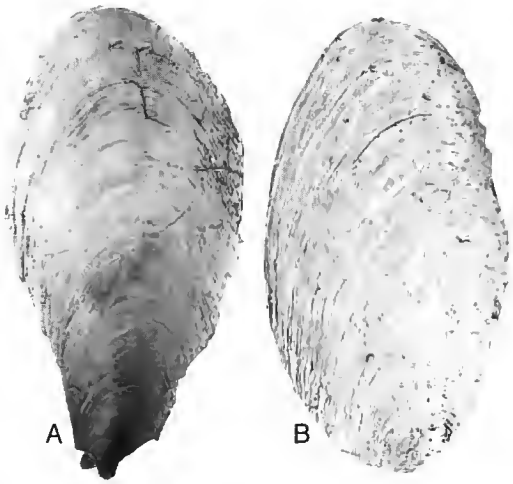

FIG. 2. — Opercula: A, *Cantharus septemcostatus* n.sp., north of New Caledonia, SMIB 6, stn DW128, 12.3 mm; B, *Cancellopollia gracilis* n.sp., Norfolk Ridge, Stylaster Bank, CHALCAL 2, stn DW76, 8.1 mm.

DESCRIPTION (Holotype)

Shell large, ovate, consisting of 1.2 protoconch and 6.0 teleoconch whorls, constricted slightly just above siphonal canal, spire moderately high. Protoconch (Fig. 4A) smooth, with five or six crowded, broad axial ribs before terminal varix, protoconch-teleoconch discontinuity sharply demarcated. Spiral cords appear along with less crowded axial ribs on first teleoconch whorl; sculpture of last whorl consisting of seven widely separated axial folds, strongest adapically, crossed by four primary and numerous secondary spiral cords; whorl broadest at level of adapical cord, which forms shoulder; fourth (abapical) cord separated from the other three primary cords. Outer lip edge erect beyond last-formed axial fold, which does not form a distinct terminal varix; lip edge with eleven crenulations, the fourth from the abapical end being larger than the others and forming a short, blunt, labral spine; this spine located at termination of external groove immediately above fourth primary spiral cord. Siphonal fasciole rounded, sculptured with about twelve fine spiral threads; umbilical slit absent; inner side of outer lip lirate, the two adapical lirae enlarged as denticles opposite very weak parietal rib at adapical end of inner lip; columella smooth, more or less straight, with fold at base of siphonal canal; inner lip slightly erect along abapical two-thirds of its length, adherent on adapical one-third.

Background colour creamy beige, axial ribs lightly tinted with rust brown especially at shoulder angulation, two middle spiral cords white at their intersection with axials. Aperture and columella white. Rather thick periostracum with hairy projections aligned along incremental lines, hairs longest on main spiral cords.

Dimensions: holotype height 36.2 mm; diameter 23.1 mm; aperture height 23.6 mm; aperture width 12.0 mm. Other material up to 40.7 mm in height.

REMARKS

Cantharus septemcostatus is closely related to two other species, *C. leucotaeniatus* Kosuge, 1985, from the Philippines, and *C. okinawa* MacNeil, 1961, from the Pliocene of Okinawa. Together, these three species form a group characterized by having spiral sculpture consisting of four primary cords, of which the most abapical (fourth) cord is remote from the other three. A groove ending at the outer lip in a blunt labral spine lies immediately above the fourth (counted from adapical end) primary spiral cord.

Cantharus leucotaeniatus (Fig. 1C) differs from *C. septemcostatus* by having a larger number of axial folds (ten to twelve as compared to seven on the last whorl), a larger number of crenulations on the outer lip (eighteen as compared to eleven), and by having the second instead of the first primary spiral cord (counting from the suture) marking the broadest point of whorl. *C. leucotaeniatus* also reaches a slightly larger size (60 mm *vs* 40.7 mm) and is more vividly coloured, with spiral cords dark brown over a white background. *C. okinawa* is extremely similar to *C. leucotaeniatus*, but has nine or ten axial folds (compared to ten to twelve), twelve instead of fifteen to eighteen crenulations and lirae on the outer lip, and an adherent instead of abapically minutely erect inner lip. The fossil species reaches a maximum length of only 29.4 mm as compared to 60 mm for *C. leucotaeniatus*. It may be that, as more material becomes available, *C. leucotaeniatus* will prove to be a junior synonym of *C. okinawa*. MacNeil (1961) described

C. okinawa from the Shinzato Tuff (Pliocene) in the Shimajiri Group of Okinawa. A. J. Kohn (pers. comm.) has collected additional specimens from the underlying Yonabaru Formation (Early Pliocene) in Okinawa. Examination of these specimens reveals that they agree in every detail with MacNeil's shells. *C. okinawa* differs from *C. septemcostatus* by having a larger number of axial folds (nine or ten instead of seven), by having the inner lip adherent instead of abapically minutely erect, and by being somewhat smaller (height 29.4 mm instead of 40.7 mm).

A probable fourth species in this group is represented by a single well-preserved fossil specimen (Fig. 1B) from the Pleistocene of Fiji, collected by A. J. Kohn. Although the spire is broken, the last whorl is perfectly preserved. It bears eight sharply rounded axial folds, crossed by six primary spiral cords. The groove terminating at the outer lip in a blunt labral tooth is located just above the lowest primary spiral cord. There are eighteen crenulations and lirae on the outer lip, of which four are situated below the crenulation that is enlarged to form the labral tooth. This specimen represents the easternmost occurrence of the genus *Cantharus*. With only a single specimen at hand, we prefer to postpone formal description until more material becomes available.

Cantharus leucotaeniatus Kosuge, 1985
(Fig. 1C)

C. albozonatus Kosuge, 1983: 137 (non *Cantharus* [*Tritonidea*] *albozonatus* Smith, 1890).

Cantharus leucotaeniatus Kosuge, 1985: 20 (nom.nov. pro *C. albozonatus* Kosuge, 1983, *non* Smith, 1890).

NEW RECORD. — **Vanuatu**. Off Espiritu Santo, MUSORSTOM 8, stn CP 1102, 15°04'S, 167°09'E, 208-210 m, 1 lv juv.

This new record represents a considerable extension of the known range, otherwise restricted to the Philippines (Springsteen & Leobrera 1986: 166).

Genus *Pollia* Gray *in* Sowerby 1834

Pollia pellita n.sp.
(Fig. 4A-C)

TYPE MATERIAL. — Holotype (lv) and 2 paratypes (dd) in MNHN.

TYPE LOCALITY. — New Caledonia, Loyalty Ridge, 20°42'S, 167°00'E, 270 m (R.V. *Alis*, MUSORSTOM 6, stn CP400).

ETYMOLOGY. — Latin *pellitus* (adj.), dressed with furs; with reference to the thick hairy periostracum of living specimens.

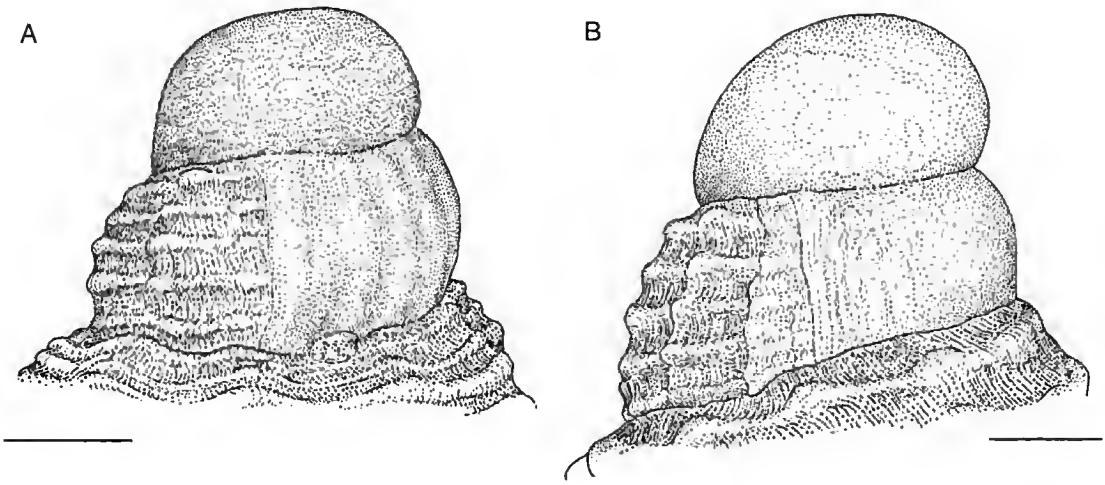

FIG. 3. — Protoconchs; **A**, *Cantharus septemcostatus* n.sp., north of New Caledonia, SMIB 6, stn DW129; **B**, *Cancellopollia gracilis* n.sp., Norfolk Ridge, Stylaster Bank, CHALCAL 2, stn DW76. Scale bars: A, B, 0.5 mm.

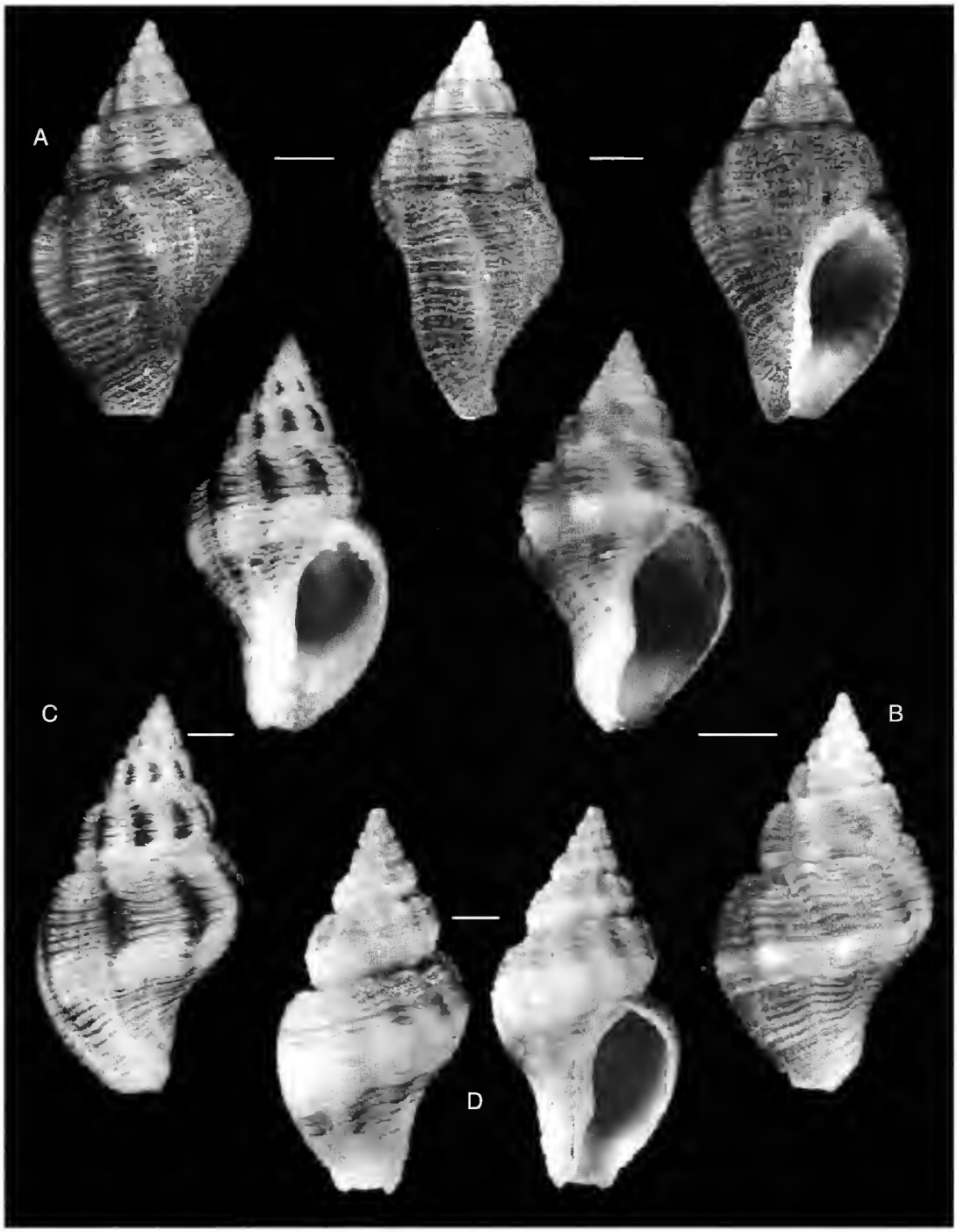

FIG. 4. — *Pollia*; **A-C**, *P. pellita* n.sp.; **A**, **B**, Loyalty Ridge, holotype, 26.5 mm (A) and paratype, 29 mm (B); **C**, Coral Sea, MUSORSTOM 5, stn 260, 33.5 mm; **D**, *P. vicdani* (Kosuge, 1984), Vanuatu, off Espiritu Santo, MUSORSTOM 8, stn DW1097, 19.8 mm.

MATERIAL EXAMINED. — **Loyalty Ridge.** MUSORSTOM 6, stn CP400, 20°42'S, 167°00'E, 270 m, 1 lv (holotype), 2 dd (paratypes).

Coral Sea. MUSORSTOM 5, stn 260, Capel Bank, 25°59'S, 159°44'E, 285 m, 1 dd. — Stn 275, Argo Bank, 24°47'S, 159°40'E, 285 m, 1 lv.

DISTRIBUTION. — Loyalty Ridge and Lord Howe Rise, alive at 270-285 m. Not found around New Caledonia proper or on the Norfolk Ridge.

DESCRIPTION

(Type material from Loyalty Ridge, Fig. 4A, B) Shell up to 29 mm in height, slender, fusiform, consisting of 2.0 protoconch and up to 6.1 teleoconch whorls. Protoconch diameter 2000 µm, exposed height 2080 µm, high, bulbous, with small nucleus, diameter 250 µm, whorls convex with deep suture, smooth, protoconch-teleoconch discontinuity distinct. Teleoconch spire whorls evenly convex on most exposed part, abapical part with narrow concave gutter, suture impressed, last whorl evenly convex to tapering base. Sculpture consisting of strong, broad axial ribs, crossed over by well-defined spiral cords. Eight axial ribs on all teleoconch whorls, interspaces narrower than ribs, with strong incremental lines. Spiral cords uneven, narrower than interspaces, main cords increasing from four on first whorl to nine on penultimate whorl, interspaces with one or two thinner secondary cords; one cord stronger, situated low on spire whorls, overhanging suture, equal to other cords and situated on periphery on last whorl; last whorl with *ca.* twenty primary cords extending onto siphonal canal, interspaces with one to four (most frequently one to three) secondary cords, some of these almost as strong as primary cords. Outer lip erect beyond external terminal varix, with thirteen internal lirae, adapical and abapical crenulations slightly enlarged, tenth lira (counted from adapical side) prolonged as a small labral tooth; inner lip erect, with *ca.* fifteen lirae corresponding to position of main cords below, parietal wall marked by two thickened folds, columella with bifid terminal swelling; aperture broad, tapering adapically; siphonal canal short but distinctly set off. No umbilicus. Background colour orange brown, spiral cords darker, white spiral band just below periphery. Periostracum very thick, tightly adhering, with long hairy expansions aligned along spiral cords.

Holotype height 26.6 mm, diameter 14.5 mm; aperture height 15 mm, aperture width 7 mm.

REMARKS

The two specimens from the Coral Sea (Fig. 4C) differ from the three type specimens by reaching a slightly larger size (up to 34 mm), details of the sculpture (nine, rather than eight, axial ribs per whorl), and a sharper colour pattern of dark brown ribs contrasting against light background. These differences could be indicative of genetical isolation of the two groups of populations, but the material is too scanty to speculate further on these differences. We prefer to provisionally treat them as geographical variants of a single biological species.

Pollia pellita differs from *P. vicdani* (Fig. 4D; Bouchet & Warén 1986: fig. 63) by being proportionally distinctly broader (*pellita* h/D = 1.77-1.90, mean 1.82, n = 5; *vicdani* h/D = 1.95-2.15, mean 2.03, n = 9) and with a smaller rib number (eight or nine *vs* fifteen per adult whorl in specimens of 26-34 mm).

Pollia vicdani (Kosuge, 1984) n.comb.
(Fig. 4D)

Cantharus vicdani Kosuge, 1984: 146, pl. 49, figs 6-9.

NEW RECORDS. — **Vanuatu.** Off Espiritu Santo, MUSORSTOM 8, stn DW1097, 15°05'S, 167°11'E, 281-288 m, 1 dd. — Stn DW1106, 15°05'S, 167°12'E, 305-314 m, 2 dd.

REMARKS

We have not examined the type material (holotype from Bohol, Philippines, in 220 m), but we have seen several lots from the Philippines [MNHN (Bouchet & Warén 1986: 471, fig. 63, as *Cantharus delicatus*), NM] that conform the original description and illustration. The status of *Cantharus vicdani* in relation to *Tritonidea delicata* Smith, 1899 is unclear. Boucher & Warén (1986: fig. 62) illustrated the holotype of *T. delicata* from the Gulf of Bengal in 165 m, and recorded the species from the Mozambique Channel and the Philippines. We have reexamined the Philippines material, which differs from

the type material of *T. delicata* by its strong axial sculpture extending over the whole whorl height. The general shell proportions are however similar and these specimens might represent local variants of a single biological species. Without further evidence, we prefer to treat the Philippines specimens as distinct from those from the Gulf of Bengal, and identify them as *C. vicdani*. The Vanuatu shells beat a general resemblance to the Philippines shells, but appear to be adult at a smaller size (19.8-20.5 mm *vs* up to 39.6 mm) and with a correlatedly lower number (ten) of axial ribs per adult whorl. They also have a more bulbous protoconch. Obviously, more material is needed from intermediate localities to evaluate the status of the various populations.

We transfer *Cantharus vicdani* to *Pollia*, based on the position of the obsolete tooth in the middle of the outer lip of Philippines specimens.

Genus *Cancellopollia* n.g.

TYPE SPECIES. — *Cancellopollia gracilis* n.sp.

ETYMOLOGY. — Latin *cancelli*, lattice; and suffix *Pollia*, suggesting close relationship to *Pollia*; gender feminine.

DIAGNOSIS

Pisaniine buccinids of medium size having fusiform shell; teleoconch whorls evenly convex, separated by shallow suture; sculpture on last whorl consisting of numerous (eighteen or more) spiral cords, which cross fifteen or more axial ribs, giving the surface a cancellate appearance. Umbilical slit absent. Outer lip convex in profile, its edge crenulated, one to three crenulations near midpoint of outer lip slightly enlarged to form very blunt labral tooth; edge of outer lip erect, extending slightly beyond external terminal adult varix; inner side of outer lip bearing short lirae; inner lip adherent; columella smooth, with fold at base of siphonal canal; aperture narrow, tapering adapically, about three times as high as wide; parietal rib at adapical end of inner lip prominent.

Radula with central tooth moderately arched, with three strong cusps medially and eventually smaller cusps marginally; laterals with large, strong cusp between the inner and outer cusps.

REMARKS

The new genus *Cancellopollia* consists of deep-water species that appear to be closely related to *Pollia*. Characters in common with *Pollia* include the terminal adult varix, the enlarged centrally placed crenulations on the edge of the outer lip, the fusiform shape, and the tapered adapical end of the narrow aperture. Both genera have a prominent parietal tooth. *Cancellopollia* differs from *Pollia* by the much finer and more numerous spiral cords and axial riblets, by having a higher spire and more slender form, by having a relatively narrower aperture, and by having fewer lirae on the inner side of the outer lip than there are spiral cords. In *Pollia*, the number of lirae roughly corresponds to the number of cords. The species currently assigned to *Cancellopollia* have a bulbous and paucispiral protoconch, indicating non-planktotrophic development, whereas those of species assigned to *Pollia* are generally multispiral, indicating planktotrophic larval development. However, we do not consider the mode of larval development to be a generic character, and we do not exclude that further deep-water exploration may lead to the discovery of species of *Cancellopollia* with multispiral protoconch.

Buccinum cinis Reeve, 1846, from the Galapagos, which has already been placed in *Monostiolum* Dall, 1904 (Keen 1971), *Caducifer* Dall, 1904 (Skoglund 1992), and a new unnamed genus (Cernohorsky 1975), is also remotely similar to species of *Cancellopollia*. It resembles them in having a slender fusiform shell, relatively numerous (eighteen) spiral cords on the last whorl, an external terminal adult varix, a lirate outer lip, and a prominent parietal rib. It differs, however, by the structure of the spiral sculpture, in which main spiral cords are flanked by secondary cords, plus spiral threadlets in between; two twin cords form a thick subsutural fold. Axial riblets are absent, instead the spiral cords are ornamented by about twenty-five granules on the last whorl. The inner lip is raised, with irregular thickened wrinkles, and there is a strong anal tooth on the outer lip. For these reasons, we believe that the

resemblance of *Buccinum cinis* to species of *Cancellopollia* is superficial, but we cannot suggest a proper generic allocation.

Cancellopollia gracilis n.sp.
(Figs 2B, 3B, 5A, 6, 7C, D)

Cantharus sp. – Cernohorsky 1981: 998, pl. 3, fig. 21.

TYPE MATERIAL. — Holotype in MNHN; paratypes: 2 (MNHN), 1 (NMNZ), 1 (AMS), 1 (NM).

TYPE LOCALITY. — South of New Caledonia, Stylaster Bank, 23°38'S, 167°43'E, 435 m (R.V. *Coriolis*, CHALCAL 2, stn DW77).

ETYMOLOGY. — Latin *gracilis* (adj.), graceful.

MATERIAL EXAMINED. — **New Caledonia slope.** *Vauban* 1978-1979, stn 15, 22°49'S, 167°12'E, 390-395 m, 1 lv (Cernohorsky 1981).
BIOCAL: stn CP52, 23°06'S, 167°47'E, 540-600 m, 1 lv.
MUSORSTOM 4, stn DW212, 22°47'S, 167°10'E, 375-380 m, 2 lv. — Stn DW220, 22°58'S, 167°38'E, 505-550 m, 3 lv, 1 juv. dd. — Stn DW221, 22°59'S, 167°37'E, 535-560 m, 8 lv, 1 dd. — Stn DW222, 22°58'S, 167°33'E, 410-440 m, 3 lv, 1 dd. — Stn DW230, 22°52'S, 167°12'E, 390-420 m, 1 juv. lv, 1 dd.
SMIB 1, stn DW2, 22°52'S, 167°13'E, 415 m, 2 lv, 1 dd.
SMIB 2, stn DW1, 22°53'S, 167°13'E, 438-444 m, 1 dd. — Stn DW3, 22°56'S, 167°15'E, 412-428 m, 2 lv, 2 dd. — Stn DW6, 22°56'S, 167°16'E, 442-460 m, 1 lv. — Stn DW8, 22°54'S, 167°13'E, 435-447 m, 1 lv. — Stn DW9, 22°54'S, 167°15'E, 475-500 m, 1 lv, 1 dd. — Stn DW17, 22°55'S, 167°15'E, 428-448 m, 2 lv.
SMIB 3, stn DW21, 22°59'S, 167°19'E, 525 m, 2 dd. — Stn DW22, 23°03'S, 167°19'E, 503 m, 3 dd. — Stn DW26, 22°55'S, 167°16'E, 450 m, 2 lv.
SMIB 8, stn DW193-196, 22°59'-23°00'S, 167°21'-167°23'E, 491-558 m, 6 lv, 6 dd. — Stn DW197-199, 22°51'-22°52'S, 167°12'E, 408-436 m, 5 lv, 22 dd. — Stn DW200, 23°00'S, 167°21'E, 514-525 m, 2 dd.
BATHUS 2, stn DW729, 22°52'S, 167°12'E, 400 m, 5 lv, 2 dd.

Aztèque Bank. SMIB 8, stn DW189, 23°18'S, 168°06'E, 400-402 m, 1 dd.
BATHUS 3, stn DW829, 23°21'S, 168°02'E, 386-390 m, 3 dd. — Stn DW830, 23°20'S, 168°01'E, 361-365 m, 1 dd.

Stylaster Bank. CHALCAL 2, stn CP25, 23°39'S, 167°43'E, 418 m, 1 lv. — Stn DW76, 23°41'S, 167°45'E, 470 m, 6 lv (paratypes AMS, NMNZ, NM), 7 dd. — Stn DW77, 23°38'S, 167°43'E, 435 m, 6 lv (holotype), 1 dd.
SMIB 3, stn DW12, 23°38'S, 167°42'E, 470 m, 5 dd. — Stn DW13, 23°38'S, 167°42'E, 448 m, 2 lv (1 paratype MNHN), 1 dd.
SMIB 8, stn DW166, 23°38'S, 167°43'E, 433-450 m, 2 lv, 2 dd, 3 juv. dd. — Stn DW167, 23°38'S, 167°43'E, 430-452 m, 4 lv, 2 juv. lv, 3 dd, 1 juv. dd. — Stn DW168, 23°38'S, 167°43'E, 433-450 m, 2 lv, 3 dd. — Stn DW169, 23°37'S, 167°42'E, 447-450 m, 1 lv, 3 juv. lv.
BERYX 11, stn DW27, 23°37'S, 167°41'E, 460-470 m, 2 lv (1 paratype MNHN), 7 juv. lv/dd. — Stn CP32, 23°38'S, 167°43'E, 420-460 m, 1 lv. — Stn DW38, 23°38'S, 167°39'E, 550-690 m, 4 lv, 14 dd. — Stn DW39, 23°37'S, 167°40'E, 490-500 m, 2 dd.

Norfolk Ridge. BERYX 11, stn DW34, 23°33'S, 167°17'E, 560-570 m, 1 lv, 1 dd.

DISTRIBUTION. — South of New Caledonia, Norfolk Ridge, alive at 415-560 m.

DESCRIPTION

Shell up to 31.8 mm in height, slender, fusiform, consisting of 1.2 protoconch and up to 5 teleoconch whorls. Protoconch (Fig. 3B) bulbous, consisting of 1.2 whorls, paucispiral, smooth, terminating with a varix followed by a fraction of a whorl with teleoconch spiral cords sculpture already present, and a second discontinuity marking transition to teleoconch. Teleoconch whorls evenly convex separated by indistinct, appressed suture; sculpture consisting of about forty fine spiral cords crossing thirty-five axial riblets on the last whorl, and eleven cords crossing thirty-one axial ribs on the penultimate whorl; outer lip crenulate, erect beyond external terminal varix; three centrally placed crenulations on outer lip slightly ventrally and adaxially enlarged; inner side of outer lip with thirteen to eighteen lirae; inner lip adherent, its adapical end marked by a prominent parietal rib; aperture narrow, tapering adapically; siphonal canal short; umbilical slit absent.
Colour off-white with tightly adhering, light yellowish beige periostracum, forming short lamellar expansions along incremental lines.
Holotype height 30.0 mm, diameter 13.2 mm;

aperture height 19.2 mm, aperture width 6.1 mm.

Discussion

Despite a geographical distribution restricted to the northern part of the Norfolk Ridge, *Cancellopollia gracilis* exhibits major variation, and morphological extremes might easily be mistaken for separate species (Fig. 6). Numerous dredge hauls have been made between 300 and 800 m in the area considered, and we consider that the known narrow bathymetric distribution

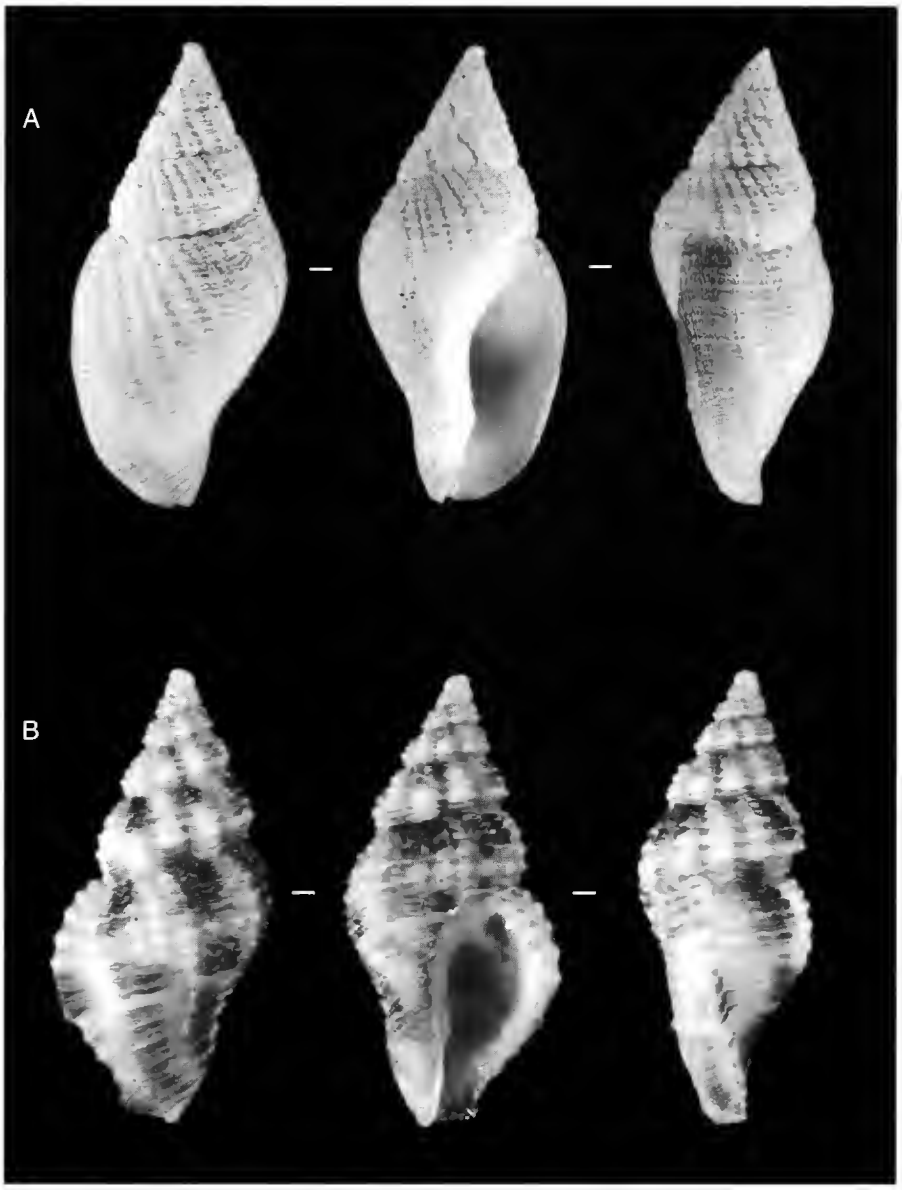

Fig. 5. — *Cancellopollia*; **A**, *C. gracilis* n.sp., Norfolk Ridge, Stylaster Bank, holotype, 30.0 mm; **B**, *C. ustulata* n.sp., Coral Sea, Chesterfield Plateau, holotype, 15.2 mm.

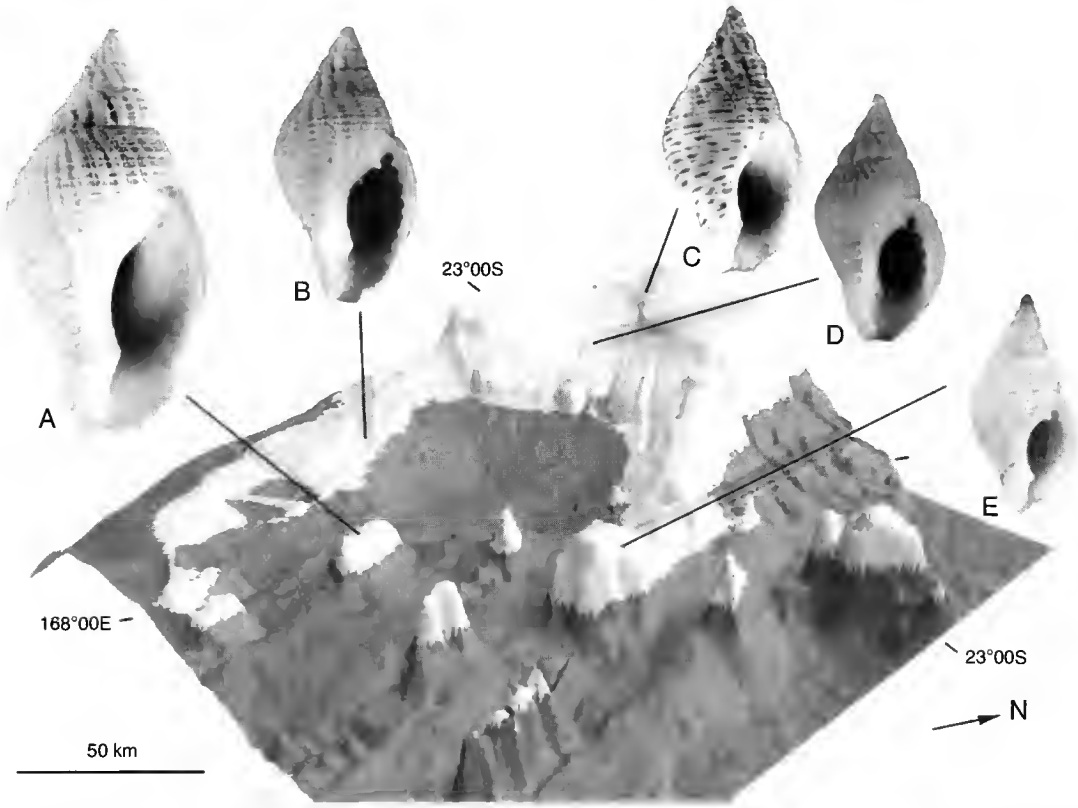

FIG. 6. — Geographical variants of *Cancellopollia gracilis* n.sp. positioned over three-dimensional bathymetry of southernmost New Caledonia and northern Norfolk Ridge. The model is positioned with the NW at top angle and the main axis of Norfolk Ridge running from the top right to lower left. Light areas are above 800 m deep, dark areas deeper than 800 m. Shell variants are printed at the same magnification. **A**, Stylaster Bank, CHALCAL 2, stn DW77, 435 m, 28.5 mm; **B**, Norfolk Ridge, BERYX 11, stn DW34, 560-570 m, 19.1 mm; **C**, New Caledonia slope, SMIB 8, stn DW197-199, 408-436 m, 18.3 mm; **D**, New Caledonia slope, SMIB 2, stn DW6, 442-460 m, 17.5 mm; **E**, Aztèque Bank, BATHUS 3, stn DW829, 386-390 m, 15.6 mm.

(415-560 m) is not a sampling artifact. Within the horizontal range are four discrete forms separated by deeper water. This, in combination with non-planktotrophic development, explains why the observed variation appears to have a strong geographical component.

1. A large number of samples originate from the slope south of New Caledonia and the Isle of Pines where bottoms at adequate depths form a continuous belt. All specimens have in common a small adult size (h = 14.9-21.1 mm) and a broad shell (h/D ratio = 1.78-2.01, mean 1.87, n = 34). Colour and sculpture are stable within a sample but show a depth-related variation. In the shallower part of the range (415-450 m), specimens have a pattern of interrupted brownish spiral cords (Fig. 6C); the axial ribs are low, almost obsolete on the last adult whorl. In the deeper part of the range (475-540 m), specimens have a uniform off-white shell (Fig. 6D); axial sculpture is much stronger and extends onto the last adult whorl.

2. Three samples originate from Aztèque Bank (Fig. 6E), a seamount to the southeast of the preceding. This population is characterized by a small adult size (h = 15.4-16.4 mm), a slender shell (h/D ratio = 1.97-2.15, mean 2.03, n = 4) with high conical spire, and a colour pattern with at least a few brownish spiral cords. Empty shells only have been dredged in 360-400 m,

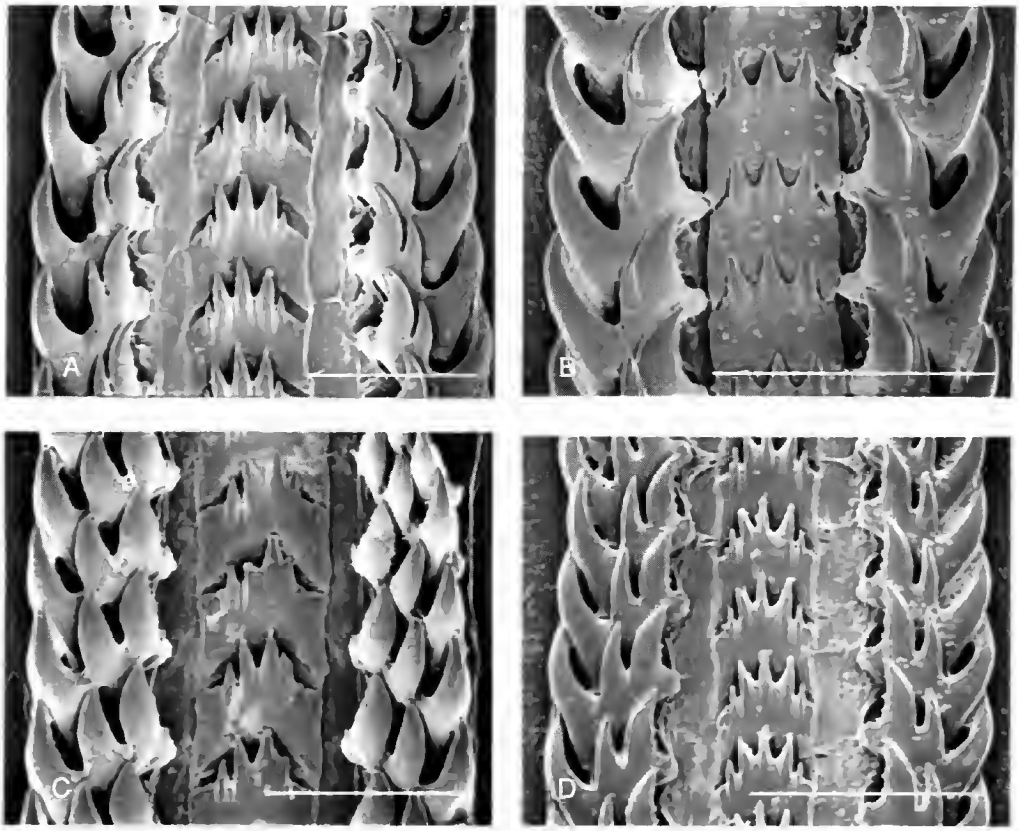

FIG. 7. — Radulae; **A**, *Cantharus septemcostatus* n.sp., north of New Caledonia, SMIB 6, stn DW128; **B**, *Cancellopollia ustulata* n.sp., Coral Sea, Chesterfield Plateau, MUSORSTOM 5, stn 379; **C**, *C. gracilis* n.sp., Stylaster Bank, CHALCAL 2, stn DW76; **D**, *C. gracilis* n.sp., New Caledonia slope, SMIB 3, stn DW26. Scale bars: 100 µm.

suggesting that *C. gracilis* lives shallower on Aztèque Seamount than elsewhere.

3. Samples from Stylaster Bank (Fig. 6A) form an isolated and homogeneous group to the south. This population is characterized by a large adult size (h = 28.0-33.7 mm), a slender shell (h/D ratio = 1.94-2.16, mean 2.09, n = 12) and a uniform off-white colour with yellowish beige periostracum.

4. Finally a single sample, with two specimens (Fig. 6B), originates from an isolated projection along the Norfolk Ridge, to the southwest. The shells look like a miniature of the Stylaster Bank form, with a much smaller adult size (h = 19.0 and 19.1 mm), broader outline (h/D ratio = 1.93), but similar sculpture and colour.

Cancellopollia ustulata n.sp.
(Figs 5B, 7B)

TYPE MATERIAL. — Holotype and 3 paratypes in MNHN.

TYPE LOCALITY. — Coral Sea, Chesterfield Plateau, 19°53'S, 158°38'E, 400 m (MUSORSTOM 5, stn 361).

ETYMOLOGY. — From the Latin *ustulatus* (adj.), a little brown as a result of burning, with reference to the brownish colour patches.

MATERIAL EXAMINED. — MUSORSTOM 5, stn 361, 19°53'S, 158°38'E, 400 m, 1 lv (holotype). — Stn 379, 19°53'S, 158°40'E, 370-400 m, 2 lv, 1 dd (paratypes).

DESCRIPTION

Shell up to 16.0 mm in height, slender, fusiform, consisting of 1.2 protoconch and five teleoconch whorls. Protoconch bulbous, paucispiral, smooth, protoconch-teleoconch discontinuity distinct. Teleoconch whorls evenly convex separated by shallow, impressed suture. Sculpture consisting of strong, broad axial ribs, crossed over by well-defined spital cords. Axial ribs eleven on first teleoconch whorl, then nine on spire whorls, twelve on penultimate, and eighteen on last whorl, interspaces narrower than ribs. Spiral sculpture consisting of six cords on exposed patt of spire whorls, interspaces broader than cords; cord 5 (cord 1 = adapical) stronget, situated low on spire whorls, equal to othet cords and situated on periphety on last whorl; last whorl with nine evenly spaced primary cords, separated by a slightly broader interspace from another group of *ca.* ten cords on shell base, crowded on siphonal canal; secondary cords present between primary cords on last whorl. Outer lip crenulate, erect beyond external terminal varix; one crenulation slightly enlarged, situated at level of fasciole between two groups of spiral cords; inner side of outer lip with nine spirally elongated swellings; inner lip adherent, parietal wall marked by a weak but distinct lira, columella with bifid terminal swelling; aperture narrow, tapering adapically; siphonal canal short but distinctly set off. No umbilicus.

Colour off-white with irregular, axially elongated brown patches. Periostracum tightly adhering, light yellowish beige, forming short lamellar expansions along incremental lines.

Holotype height 15.2 mm, diamerer 7.3 mm; aperture height 6.5 mm, aperture width 3.1 mm.

DISCUSSION

Cancellopollia ustulata differs from *C. gracilis* by its smaller adult size, more slender spire with more convex spire whorls, coarser axial and spiral sculpture, with fewer ribs and cords, and correlatedly fewer apertural lirae. It also differs from the coloured individuals of *C. gracilis* by the brown colour forming distinctly axial blotches, rather than spirally discontinuous cords.

C. ustulata is known only from the slope of the Chesterfield Plateau, a mid-Tertiary isolated structure in the middle of the Coral Sea, separated from New Caledonia and Australia by abyssal depths.

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A new species of *Tityus* C. L. Koch, 1836 (Scorpiones, Buthidae) in Colombia, with a check list and key to the Colombian species of the genus

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Lourenço W. R. 1998. — A new species of *Tityus* C. L. Koch, 1836 (Scorpiones, Buthidae) in Colombia, with a check list and key to the Colombian species of the genus. *Zoosystema* 20 (3) : 487-497.

KEY WORDS
Scorpiones, Buthidae, *Tityus oteroi* n.sp., Darién, Colombia, new species, check list, taxonomic key.

ABSTRACT

Tityus oteroi n.sp. (Scorpiones, Buthidae) is described on the basis of five specimens (one male and four females), collected in the region of Darién in the north of Colombia. With the description of *Tityus oteroi*, the number of species of the genus *Tityus* known to be distributed in Colombia is raised to twenty. Some comments concerning the taxonomic position of the new species are added. A check list of Columbian species of *Tityus* as well as keys for their determination are also included.

MOTS CLÉS
Scorpiones, Buthidae, *Tityus oteroi* n.sp., Darién, Colombie, nouvelle espèce, « check list », clé taxonomique.

RÉSUMÉ

Une nouvelle espèce du genre Tityus *C. L. Koch, 1836 (Scorpiones, Buthidae) de Colombie, avec une liste complète et des clés pour les espèces colombiennes de ce genre. Tityus oteroi* n.sp. (Scorpiones, Buthidae) est décrit à partir de cinq exemplaires (un mâle et quatre femelles), collectés dans la région de Darién au nord de la Colombie. Avec la description de *Tityus oteroi*, le nombre d'espèces appartenant au genre *Tityus*, connues pour la Colombie s'élève à vingt. Quelques commentaires sur la position taxonomique de la nouvelle espèce sont ajoutés. Sont également incluses une liste des espèces colombiennes de *Tityus*, ainsi que des clés pour leur détermination.

INTRODUCTION

The Colombian scorpion fauna has attracted the attention of arachnologists since the middle of the 19th century (*e.g.* Gervais 1844; Thorell 1876; Pocock 1893; Kraepelin 1912, 1914; Mello-Leitão 1945). Only since the 1980s, however, and especially during the last ten years has this fauna been studied intensively. Several new species have been added (Lourenço 1984a, b, 1991, 1993, 1994, 1995a, b; Lourenço & Florez 1989, 1990a, b, 1995). A more recent contribution by Lourenço (1997) represented the first attempt to produce a summary of this fauna associated with biogeographical considerations. It was admitted, however, that the results of this summary are tentative, and that a number of additional species should exist in Colombia. A much larger inventory will reveal a more realistic number of taxa present in the country. At present, a total of four families (Buthidae, Chactidae, Diplocetridae and Ischnuridae), nine genera, and forty-one species has been confirmed for Colombia.

Recent study of old specimens collected in the region of Darién by F. Geay back in 1899 and deposited in the collections of the Muséum national d'Histoire naturelle, Paris, revealed one more new species of *Tityus* in Colombia. Moreover, because many people have been stung by scorpions in this country during the last few years, probably by species belonging to the genus *Tityus*, it seemed useful to present a check list and keys to the species known to be present in Colombia.

SYSTEMATICS

Genus *Tityus* C. L. Koch, 1836
Tityus oteroi n.sp.
(Figs 1-3)

HOLOTYPE. — **Colombia.** Darién, 1899, F. Geay leg.: ♂, deposited in the MNHN, Paris (RS-0853).

ETYMOLOGY. — Patronym in honour of Dr. Rafael Otero Patiño of the Universidad de Antioquia, Colombia.

TABLE 1. — Measurements (in mm) of *Tityus oteroi* n.sp.

	Holotype ♂	Allotype ♀
Carapace:		
length	8.7	9.2
anterior width	6.8	7.2
posterior width	9.4	10.6
Metasoma, segment I:		
length	6.4	5.8
width	4.3	5.0
Metasoma, segment V:		
length	10.5	9.6
width	4.5	5.0
depth	4.4	4.3
Vesicle:		
width	3.6	3.6
depth	3.4	3.3
Femur:		
length	16.2	10.2
width	2.7	2.6
Tibia:		
length	16.3	10.8
width	3.2	3.7
Chelae:		
length	25.7	19.2
width	2.5	3.5
depth	2.5	3.6
Movable finger:		
length	15.2	12.6

MEASUREMENTS. — See Table 1.

DESCRIPTION OF MALE HOLOTYPE

Coloration

Base colour blackish-brown. Prosoma: carapace blackish-brown; coxosternal region yellowish-brown. Mesosoma: dorsum blackish-brown with two confluent yellowish lateral stripes. Venter yellowish-brown. Metasoma: segments I to IV blackish-brown; V darker, more blackish. Vesicle: reddish-black. Chelicerae yellowish-brown with a very dark thread; fingers dark. Pedipalps: palm reddish-yellow; fingers reddish-brown. Legs reddish-brown with diffuse fuscous spots.

Morphology

Carapace moderately granular; anterior margin

with a median concavity. Anterior median, superciliary, and posterior median keels moderate to strong. All furrows moderately deep. Median ocular tubercle distinctly anterior to centre of carapace. Eyes separated by more than one ocular diameter. Three pairs of lateral eyes. Sternum subtriangular. Mesosoma: tergites moderately granular. Median keel strong on all tergites; tergite VII pentacarinate. Venter: genital operculum divided longitudinally. Pectines: pectinal tooth count 20-21; basal middle lamellae of the pectines not dilated. Sternites smooth with elongate stigmata; sternite VII with four very feeble keels. Metasoma: segments I to IV with dorsolateral keels serrate and lateral supramedian keels crenulate. Dorsolateral keels on segments II to IV with numerous strongly spinoid granules (this character is diagnostic for the new species) (Fig. 1A). Lateral inframedian keels on segment I complete, strongly crenulate; on segments II and III represented by only two to three distal granules; absent on segment IV. Ventrolateral and ventral submedian keels strong, crenulate. Intercarinal spaces moderately granular. Segment V with dorsolateral and latetomedian keels vestigial; ventrolateral and ventromedian keels strong, crenulate. Lateral intercarinal spaces moderately granular. Telson, feebly granular, almost smooth with a long and strongly curved aculeus. Dorsal surface smooth; ventral surface feebly granular; subaculear tooth moderate and spinoid. Cheliceral dentition characteristic of the family Buthidae (Vachon 1963); ventral aspect of both fingers and manus with long dense setae. Pedipalps: femur pentacarinate; tibia with six to seven keels; chelae with vestigial keels; all faces feebly granular, almost smooth. Movable fingers with 16-16 oblique rows of granules. Trichobothriotaxy: orthobothriotaxy A-α (Vachon 1973, 1975; Figs 2, 3). Legs: tarsus ventrally with numerous short fine setae.

DESCRIPTION OF ALLOTYPE AND PARATYPES

One allotype (female) and three paratypes

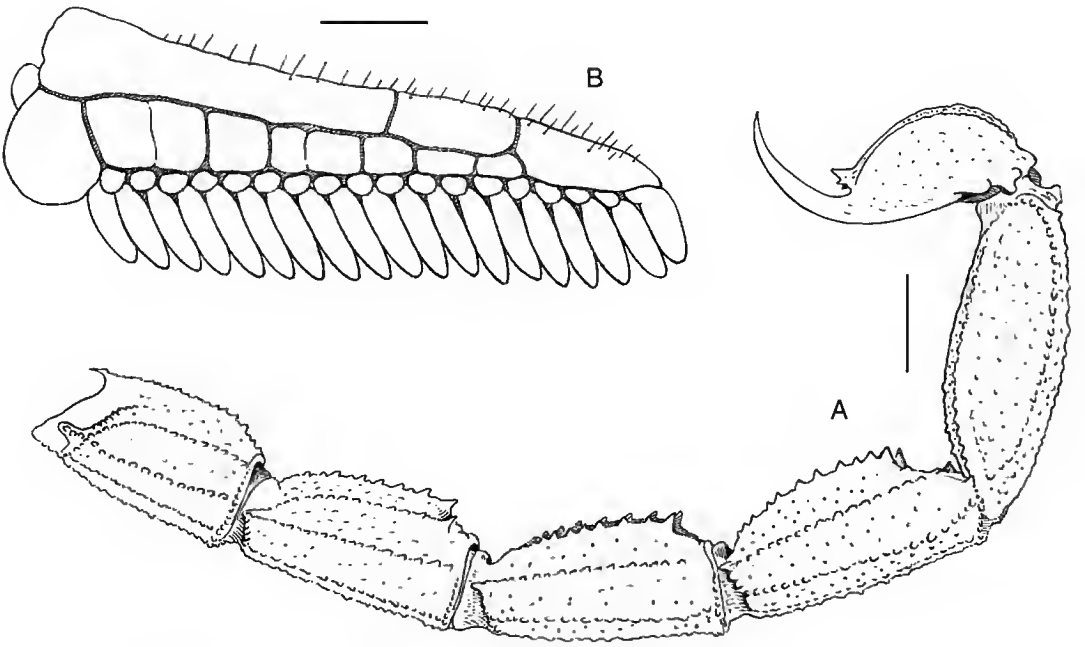

FIG. 1. — **A**, *Tityus oteroi* (♂ holotype); metasoma, lateral aspect, showing the carinal structure and the spinoid dorsal granules; **B**, *Tityus oteroi* (♀ allotype); pecten. Scale bars : A, 4 mm; B, 2 mm.

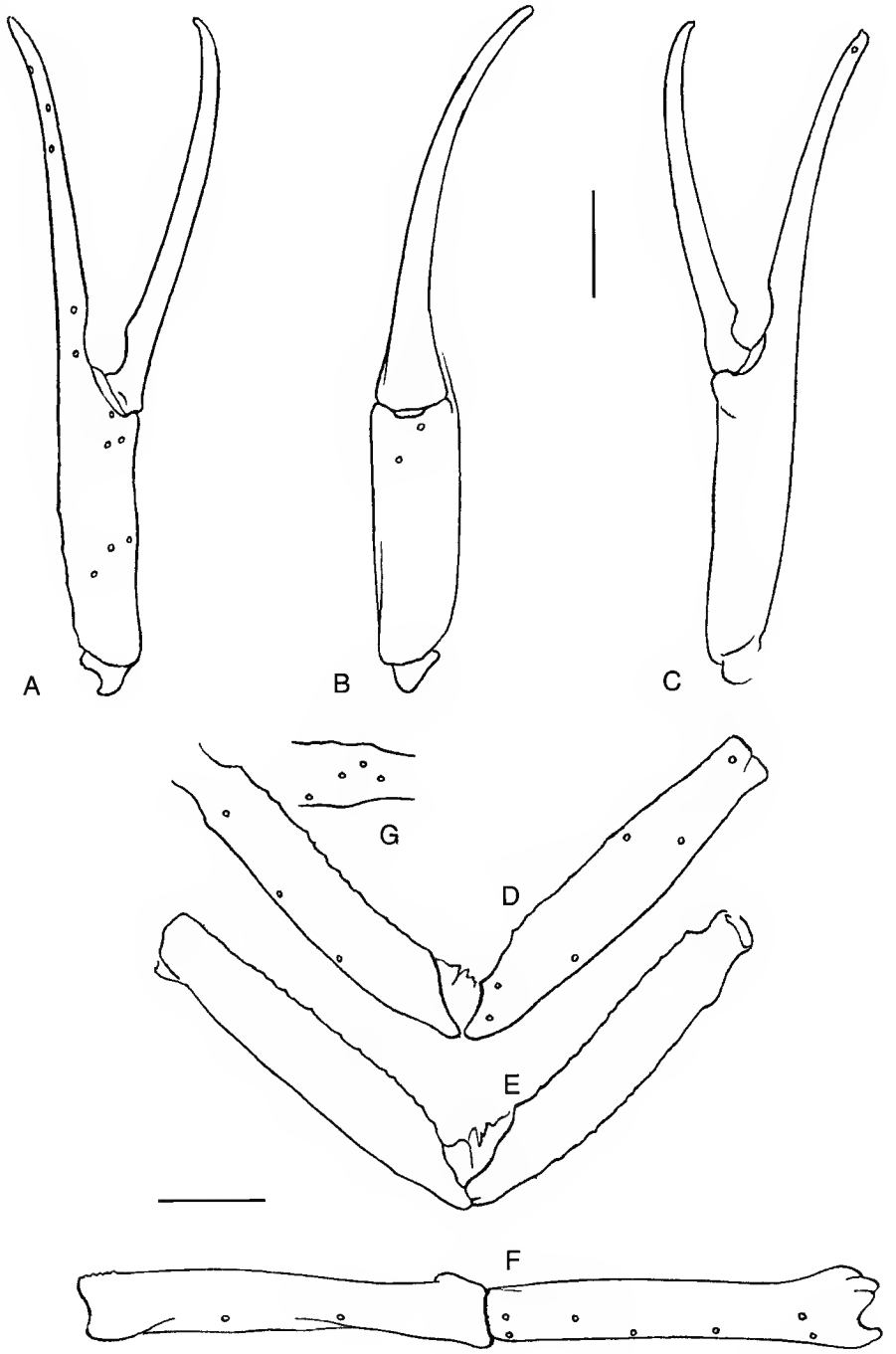

Fig. 2. — Trichobothrial pattern of *Tityus oteroi* (♂ holotype); **A-C**, chela, external, ventral and internal aspects; **D-F**, femur and tibia, dorsal, ventral and external aspects; **G**, detail of left pedipalp femur with dorsal trichobothria. Scale bars: 4 mm.

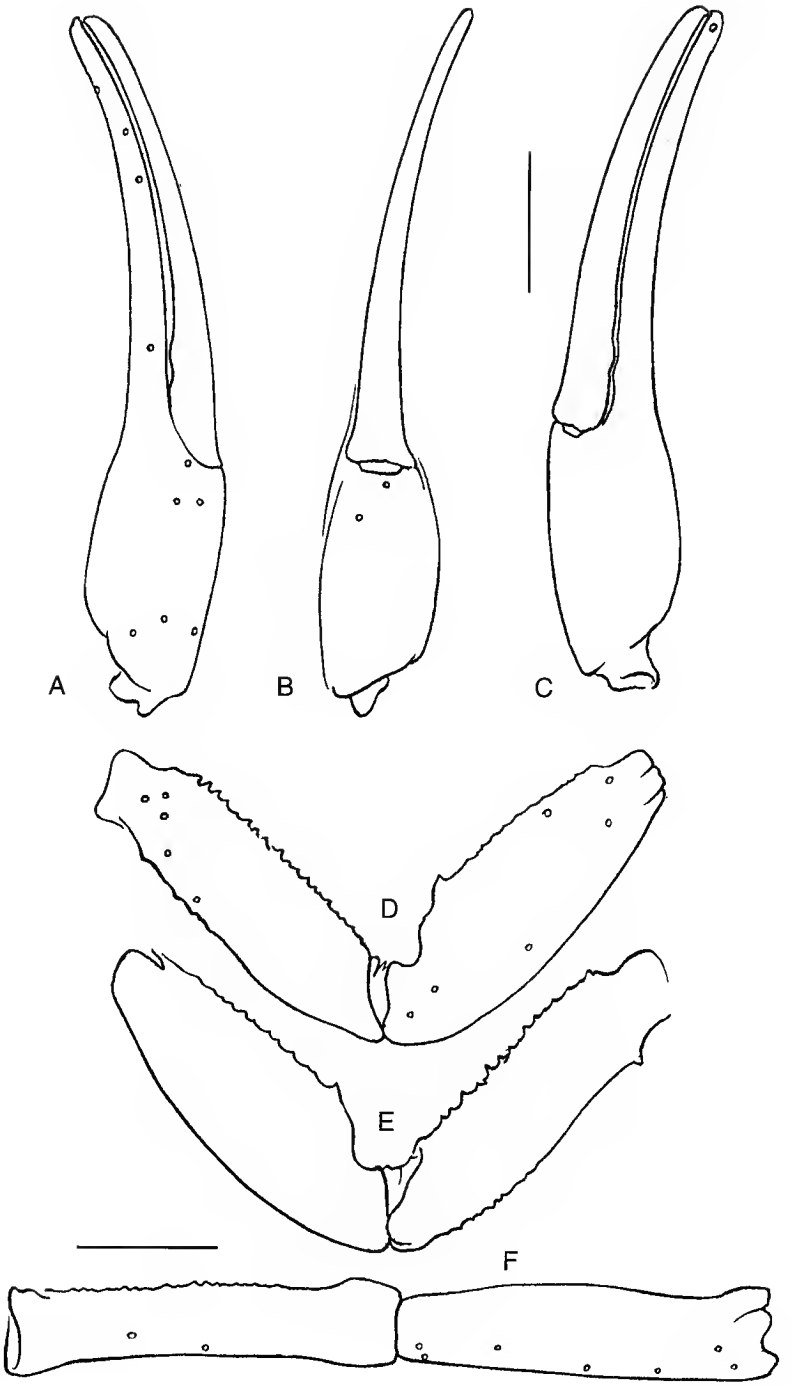

FIG. 3. — Trichobothrial pattern of *Tityus oteroi* (♀ allotype); **A-C**, chela, external, ventral and internal aspects; **D-F**, femur and tibia, dorsal, ventral and external aspects. Scale bars: 4 mm.

(females) with same data as for the holotype. Coloration similar to that of the holotype, only slightly darker. General morphology different to that of the holotype by mophometric values (see Table 1). Female pectines smaller, with 19-19 (allotype), 18-19, 19-20, 20-20 teeth; basal middle lamellae strongly dilated (Fig. 1B).

TAXONOMIC POSITION

The new species belongs to the "*Tityus asthenes*" group. It is closely associated with *Tityus nematochirus* Mello-Leirão, 1940; however, it can readly be distinguished from this last species by rhe presence of the strongly spinoid granules on the dorsal keels of metasomal segments II to IV. In *T. nematochirus* these keels are poorly carinated and the granules are round and smooth. It can be distinguished from *T. asthenes* Pocock, 1893 by having distinctly more elongated pedipalps (see taxonomic key).

CHECK LIST

Family BUTHIDAE Simon, 1880
Genus *Tityus* Koch, 1836

Species belonging to the "*Tityus clathratus*" group:
Tityus bastosi Lourenço, 1984
T. betschi Lourenço, 1992
T. columbianus (Thorell, 1876)
T. tayrona Lourenço, 1991

Species belonging to the "*Tityus bahiensis*" group:
Tityus blanci Lourenço, 1994
T. charalaensis Mello-Leitão, 1940
T. engelkei Pocock, 1902
T. lourençoi Florez, 1995
T. rebierei Lourenço, 1997
T. sabineae Lourenço, 1994
T. sastrei Lourenço *et* Florez, 1990

Species belonging to the "*Tityus asthenes*" group:
Tityus asthenes Pocock, 1893
T. cuellari Lourenço, 1994
T. festae Borelli, 1899
T. forcipula (Gervais, 1844)
T. fuhrmanni Kraepelin, 1914
T. macrochirus Pocock, 1897
T. nematochirus Mello-Leitão, 1940
T. oteroi n.sp.
T. pachyurus Pocock, 1897

Total: 20 species (see also map Fig. 4).

DIAGNOSIS OF THE GENUS *Tityus* Koch, 1836 WITH KEYS TO THE SPECIES KNOWN FROM COLOMBIA

Scorpions of small, medium or large size ranging from 25 to 110 mm in total length. The general coloration can present almost all the colour patterns that are observed among scorpions in general, ranging from pale-yellowish or reddish-yellow to reddish-brown, dark-brown and blackish, and with dark spots which may be distributed in many different configurations. All segments are in general strongly granulated. Dentate margins of pedipalp-chela fingers composed of twelve to seventeen oblique rows of granules, but with supernumerary granules not present. Pectine teeth ranging in number from ten to thirty. Metasomal segments parallel in both males and females or elongated or enlarged posteriorly in males. Sexual dimorphism present in almost all species, and with several different patterns or configurations.

KEY TO THE THREE GROUPS OF *Tityus* PROPOSED IN THE CHECK LIST

1. Small species ranging from 25 to 40 mm in total length with variegated pigmentation and a rhomboidal subaculear tooth ..... *Tityus clathratus* group

— Species of medium or large size, ranging from 50 to 100 mm in total length; pigmentarion varying from yellowish to brown and black; subaculear tooth spinoid .. 2

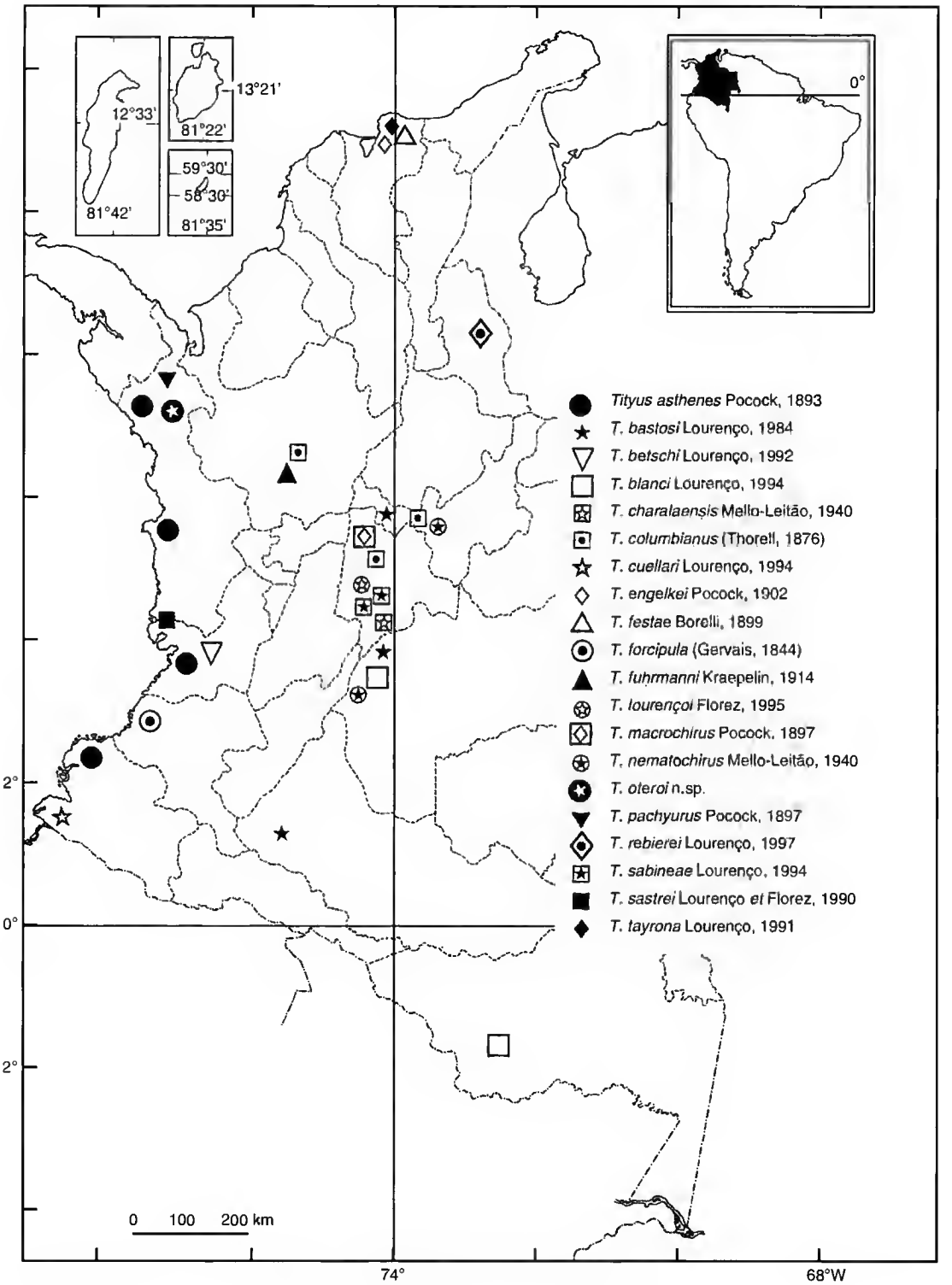

FIG. 4. — Known distribution of the *Tityus* species in Colombia.

2. Species of medium size, ranging from 50 to 70 mm in total length; coloration rather pale varying from yellowish to reddish-brown or brownish, never black; often with conspicuous dark spots; basal middle lamellae of female pectines not dilated in almost all species ..... *Tityus bahiensis* group

— Species of large size, ranging from 65 to 100 mm in total length; pigmentation blackish in the adult and yellowish/variegated in immature individuals; subaculear tooth always spinoid; basal middle lamellae of female pectines dilated in almost all species ..... *Tityus asthenes* group

KEY TO THE SPECIES OF THE *Tityus clathratus* GROUP

1. Dorsolateral keels of metasomal segments I to IV without a spinoid posterior granule or with only a very feeble granule 2

— Dorsolateral keels of metasomal segments I to IV with a strong spinoid posterior granule; Amazonia ..... *T. bastosi*

2. Subaculear tooth strong and very rhomboidal 3

— Subaculear tooth moderate and feebly rhomboidal ..... *T. betschi*

3. Pectines with ten to fourteen teeth ..... *T. columbianus*

— Pectines with fourteen to seventeen teeth ..... *T. tayrona*

KEY TO THE SPECIES OF THE *Tityus bahiensis* GROUP

1. Ventral submedian keels of metasomal segments III and IV converging proximally to form a Y shape ..... *T. rebierei*

— Ventral submedian keels of metasomal segments III and IV parallel through entire length 2

2. General coloration from yellowish to reddish-yellow 3

— General coloration from dark-reddish to blackish 5

3. Dorsolateral keels of metasomal segments II to IV with several granules modified as spines ..... *T. blanci*

— Dorsolateral keels of metasomal segments II to IV without granules modified as spines 4

4. Basal middle lamellae of female pectines strongly dilated; dentate margins of pedipalp-chela fingers composed of thirteen to fourteen oblique rows of denticles .... *T. engelkei*

— Basal middle lamellae of female pectines not dilated; dentate margins of pedipalp-chela fingers composed of sixteen oblique rows of denticles ..... *T. sastrei*

5. Male pedipalps slightly longer and more slender than those of females 6

— Male pedipalps larger and more bulky than those of females ..... *T. sabineae*

6. Pectines with sixteen to seventeen teeth; dentate margins of pedipalp-chela fingers composed of seventeen oblique rows of denticles ..... *T. lourençoi*

— Pectines with fourteen teeth; dentate margins of pedipalp-chela fingers composed of twelve oblique rows of denticles ..... *T. charalaensis*

KEY TO THE SPECIES OF THE *Tityus asthenes* GROUP

1. Male pedipalps longer and more slender than those of females 2

— Male pedipalps larger and more bulky than those of females 4

2. Values of (male) femur, tibia and chelae length respectively 6/8, 8/10 and 10/13 times longer than width 3

— Values of (male) femur, tibia and chelae length respectively 5, 3 and 5 times longer than width ..... *T. asthenes*

3. Dorsolateral keels of metasomal segments I to IV with several strong spinoid posterior granules ..... *T. oteroi*

— Dorsolateral keels of metasomal segments I to IV without spinoid posterior granules ..... *T. nematochirus*

4. Dorsolateral keels of metasomal segments I to IV with several strong spinoid posterior granules, or with one very strong spinoid posterior granule 5

— Dorsolateral keels of metasomal segments I to IV with moderate or feeble spinoid posterior granules 7

5. One very strong spinoid posterior granule on dorsolateral keels of metasomal segments II to IV ..... *T. fuhrmanni*

— Several strong spinoid posterior granules on dorsolateral keels of metasomal segments I to IV 6

6. Adult size around 60 mm; legs and pedipalps blackish ..... *T. forcipula*

— Adult size around 45 mm; legs and pedipalps yellowish to reddish-yellow ..... *T. cuellari*

7. Moderate spinoid posterior granules on dorsolateral keels of metasomal segments I to IV; male pedipalps larger and more bulky than those of females ..... *T. pachyurus*

— Feeble spinoid posterior granules on dorsolateral keels of metasomal segments I to IV; male pedipalps only slightly larger and more bulky than those of females 8

8. Pectines with fifteen to sixteen teeth; dentate margins of pedipalp-chela fingers composed of fifteen oblique rows of denticles ..... *T. macrochirus*

— Pectines with twenty-one to twenty-two teeth; dentate margins of pedipalp-chela fingers composed of sixteen oblique rows of denticles ..... *T. festae*

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Réhabilitation du genre *Harmonicon* (Pickard-Cambridge, 1896) et description d'une nouvelle espèce de Guyane française (Araneae, Mygalomorphae, Dipluridae)

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Maréchal P. & Marty C. 1998. — Réhabilitation du genre *Harmonicon* (Pickard-Cambridge, 1896) et description d'une nouvelle espèce de Guyane française (Araneae, Mygalomorphae, Dipluridae). *Zoosystema* 20 (3) : 499-504.

MOTS CLÉS
Araneae, Mygalomorphae, Dipluridae, Guyane française, nouvelle espèce, *Harmonicon*.

RÉSUMÉ

Une nouvelle espèce de la famille des Dipluridae est décrite de Guyane française. Ses affinités avec une espèce brésilienne conduisent à la réhabilitation du genre *Harmonicon* (Pickard-Cambridge, 1896). Quelques éléments de la biologie de cette nouvelle espèce sont exposés.

KEY WORDS
Araneae, Mygalomorphae, Dipluridae, French Guiana, new species, *Harmonicon*.

ABSTRACT

Reinstatement of the genus Harmonicon *(Pickard-Cambridge, 1896) with description of a new species from French Guiana (Araneae, Mygalomorphae, Dipluridae).* A new species of the Dipluridae family is described from French Guiana. Its affinities with a Brasilian species lead to the reinstatement of the genus *Harmonicon* (Pickard-Cambridge, 1896). Some biological aspects of this new species are described.

INTRODUCTION

Dans son dernier travail consacré aux araignées de la Guyane française, Caporiacco (1954) recense trois espèces de la famille des Dipluridae. Poursuivant l'étude systématique de la faune mygalomorphe de ce département d'outre-mer récemment entreprise (Maréchal 1996), nous décrivons ici une nouvelle espèce de cette famille. Cette donnée inédite nous conduit à revenir sur certaines synonymies établies par Raven (1985) au sein de la sous-famille des Diplurinae et plus particulièrement dans le genre *Diplura*.

Les informations écologiques et comportementales collectées à plusieurs reprises sur le terrain permettent également de présenter quelques aspects de la biologie de cette Dipluridae guyanaise.

Les Dipluridae américaines

La famille des Dipluridae comprend actuellement quatre sous-familles (Raven 1985). Parmi celles-ci, celle des Diplurinae est spécifique du continent américain et, plus précisément, de la région néotropicale. Il paraît donc tout à fait naturel de trouver de nouvelles espèces de cette sous-famille en Guyane française, département dont l'étude de la faune arachnologique est à peine entamée.

Le genre Diplura

Le genre *Diplura* a été créé par Simon (1892) sur la base de scopulae peu denses sur les tarses. Après la découverte par Pickard-Cambridge (1896) d'une lyre sur la coxa des pédipalpes chez *Melodeus*, Simon (1903) la suppose absente chez *Diplura*. Par la suite, tous les auteurs ont classé les espèces munies d'une lyre dans d'autres genres. Ce n'est que lors du travail de révision de Raven (1985) que la présence d'une lyre est constatée chez *Diplura macrura* (Koch, 1842) et que toutes les Diplurinae munies d'un tel organe, exceptées celles du genre *Trechona* (Koch, 1851), y sont rassemblées. Pas moins de onze genres, souvent monospécifiques, sont ainsi mis en synonymie par Raven (1985).

La découverte d'une mygale proche de *Diplura rufescens* (Pickard-Cambridge, 1896) et l'examen du type de cette dernière révèlent un certain nombre de différences morphologiques d'importance générique au niveau de la lyre et des pattes. Nous proposons donc la réhabilitation du genre *Harmonicon* (Pickard-Cambridge, 1896) jusqu'ici monospécifique et en décrivons une nouvelle espèce.

Genre *Harmonicon* Pickard-Cambridge, 1896

ESPÈCE-TYPE. — L'espèce-type du genre est *Harmonicon rufescens* Pickard-Cambridge, 1896.

DIAGNOSE DIFFÉRENTIELLE. — Diffère de toutes les autres Diplurinae par la formule ambulatoire 1423. Diffère de *Diplura* par des pattes proportionnellement plus longues et plus fines, la lyre dont l'extrémité des soies est aplatie et recourbée en crochet, et l'absence de protubérance sur les métatarses I des mâles adultes.

DESCRIPTION

Dipluridae de grande taille (corps supérieur à 25 mm), gracile, aux pattes longues et fines dont le rapport ambulatoire est très nettement inférieur à dix (supérieur chez les espèces du genre *Diplura*). La lyre est constituée de cinq soies, ce qui pourrait être un caractère générique. Les filières postérieures latérales sont longues et effilées.

REMARQUE

Le spécimen-type de *H. rufescens* est mutilé d'origine et la quatrième paire de pattes manque. La formule ambulatoire ne peut donc être connue. De plus, Raven (1985) considère la formule 4123 comme l'un des caractères distinctifs des Diplurinae. Les deux espèces du genre *Harmonicon* possédant par ailleurs tous les caractères de la sous-famille, ce critère ne peut être considéré comme pertinent pour caractériser les Diplurinae.

Harmonicon audeae n.sp.

MATÉRIEL EXAMINÉ. — **Guyane française.** Stn de Saint-Eugène, 4°50'N - 53°05'W, capturée le 22.X.1996, coll. de Massary : holotype ♀. — Piste de Saint-Élie, pk 10, 5°15'N - 53°05'W, capturé le 21.X.1995, coll. P. Gaucher : allotype ♂. — Stn de Saint-Eugène, capturé le 22.X.1996 : 1 ♂ ; capturé le 18.V.1996, coll. de Massary) : 1 immature. L'ensemble du matériel est déposé au Muséum national d'Histoire naturelle, Paris (MNHN).

ÉTYMOLOGIE. — Cette espèce est baptisée en l'honneur de la naissance de la fille de l'un des auteurs.

DIAGNOSE DIFFÉRENTIELLE. — Diffère de *H. rufescens* par la présence sur les tarses des pédipalpes d'une scopula et d'une griffe munie d'une double rangée de dents (femelle). Diffère également par la présence d'épines sur les fémur des pattes I et II.

DESCRIPTION

Holotype femelle

Longueur totale sans les chélicères, 33 mm.

Couleur. Céphalothorax brun orangé. Pattes, sternum et pièce labiale fauve clair, légèrement jaunâtre ou orangé. Abdomen uniformément gris violacé recouvert d'une fine pubescence grisâtre et parsemé de long poils noirs.

Carapace. Longueur 13,5 mm ; largeur 12 mm. Recouverte d'une pubescence noire clairsemée et bordée de soies noires courbées vers l'avant.

Fovéa. Petite, profonde et légèrement récurvée.

Yeux. Tubercule distinct mais peu élevé, yeux antérieurs en ligne légèrement procurvée, les postérieurs en ligne faiblement récurvée. Les yeux médians antérieurs sont les plus gros (Fig. 1A).

Chélicères. Munies d'une plage dorsale longitudinale de longs poils qui s'évase vers la base du crochet. Présence d'une bande pubescente en position dorso-latérale et d'une autre plus étroite et plus discrète en position latéro-externe. Marge interne portant neuf dents coniques en ligne terminée, dans la partie basale, par un groupe de

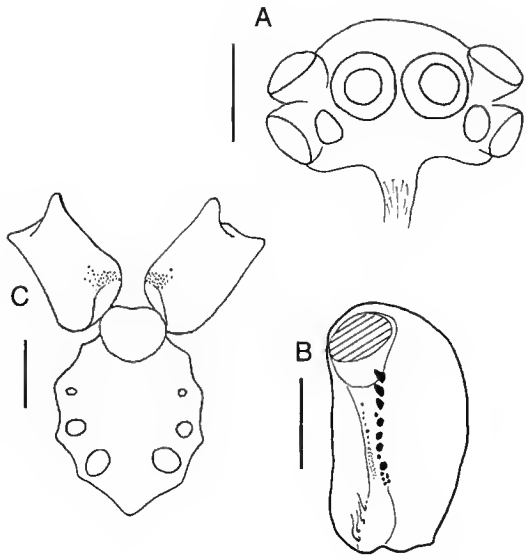
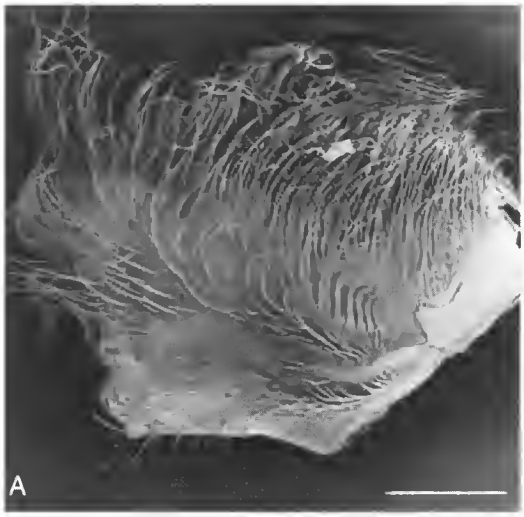


FIG. 1. — *Harmonicon audeae* n.sp., holotype ♀. **A**, aire oculaire, vue dorsale ; **B**, chélicère droite, vue ventrale ; **C**, lames maxillaires, labium et sternum, vue ventrale. Échelles : A, 1 mm ; B, C, 3 mm.



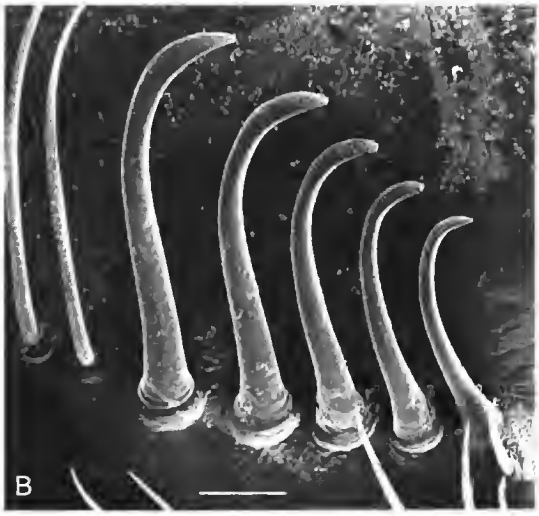


FIG. 2. — *Harmonicon audeae* n.sp., ♂, MEB ; **A**, face interne de la coxa du pédipalpe droit montrant l'emplacement de la lyre ; **B**, détail de la lyre constituée de cinq soies dont l'extrémité, aplatie, est recourbée en crochet. Échelles : A, 1 mm ; B, 100 µm.

cinq dents plus petites. Gouttière munie d'une série longitudinale de denticules qui se termine en plage dans la partie basale. De longs poils orangés et denses garnissent la marge externe qui porte quatre soies isolées dans sa partie basale (Fig. 1B).

Lames maxillaires. Longueur 4,5 mm ; largeur 3,15 mm. Munies, dans leur angle interne, de quarante à quarante-cinq denticules. Serrula présente dans la partie interne près de la marge apicale. Présence, sur la face interne, d'une lyre constituée de cinq soies dont l'extrémité, aplatie, est recourbée en crochet (Fig. 1C, 2).

Labium. Longueur 2,25 mm ; largeur 2,25 mm. De forme quadrangulaire, le labium ne porte que quelques poils épars. Pas de denticules (Fig. 1C).

Sternum. Longueur 6,6 mm ; largeur 5,7 mm. Suture labio-sternale constituée par deux larges fossettes semi-circulaires épousant le contour de la base du labium. Sigilles bien distincts, ronds et profonds. Les postérieurs sont les plus gros.

Pédipalpe. Muni d'une griffe portant, à sa base, une double rangée de six à sept dents. Présence d'une scopula peu dense mais nettement visible sur la moitié apicale du tarse. Présence de courtes trichobothries en une rangée médiane sur le tarse et en une double rangée latérale sur le tibia.

Pattes. Formule ambulatoire (classement des pattes par ordre de longueur décroissant) 1423. Pattes longues et fines, le rapport ambulatoire (diamètre du fémur/longueur totale × 100) compris entre 6,4 et 4,5. Griffes paires munies d'une double rangée de six à huit dents. Griffe impaire mutique. Tarses pseudosegmentés. Scopula peu dense séparée par une double rangée médiane de setae sur les tarses I et II. Scopula quasi inexistante et setae plus fortes sur les tarse III et IV.

Mensurations (mm)	I	II	III	IV	Pd
Fémur	14	12,5	11,5	14	8,5
Patelle	6	6	5,5	5,5	3,5
Tibia	11,5	10,5	9,5	12	7
Métatarse	11	10	12	20,5	–
Tarse	7	6,5	6,5	8	6
Total	49,5	45,5	45	60	25
Diamètre fémur	3,1	2,9	2,8	2,7	–
rapport ambulatoire	6,26	6,37	6,22	4,5	–

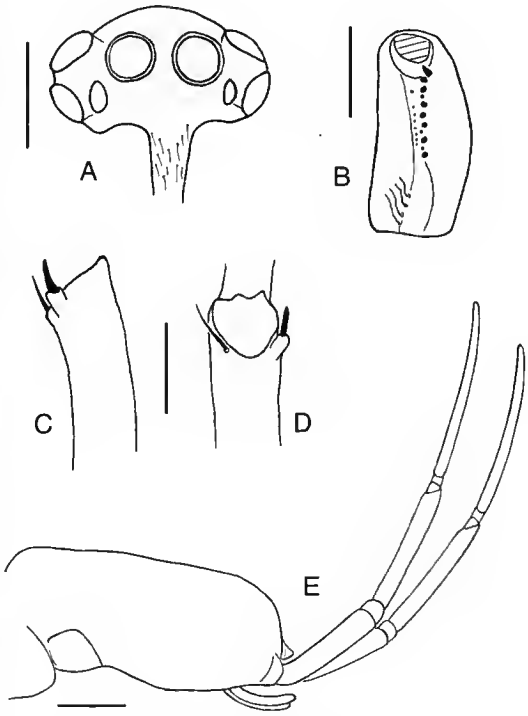


Fig. 3. — *Harmonicon audeae* n.sp., allotype ♂. **A**, aire oculaire, vue dorsale ; **B**, chélicère droite, vue ventrale ; **C** et **D**, éperon du tibia I en vue latéro-externe (C) et ventrale (D) ; **E**, abdomen et filières en vue latérale. Échelles : A, 1 mm ; B-E, 3 mm.

Présence d'une scopula clairsemée sur le métatarse I et dans le tiers apical du métatarse II.

Trichobothries longues et fines, présentes en une rangée médiane sur les tarses et les métatarses et en une double rangée latérale sur les tibias.

Épines nombreuses et très irrégulières par leur taille et leur force, présentes sur les métatarses, les tibias et les fémurs. Leur nombre et leur disposition est très variable d'un individu à l'autre et d'un côté à l'autre sur un même individu. Tarses toujours mutiques à l'exception des pédipalpes qui portent une ou deux épines sur la face ventrale.

Filières. Longueur des postérieures médianes 3,5 mm. Longueur des postérieures latérales 22,5 mm ; article basal 6,5 mm ; article médian 6,25 mm ; article apical 9,75 mm. Filières posté-

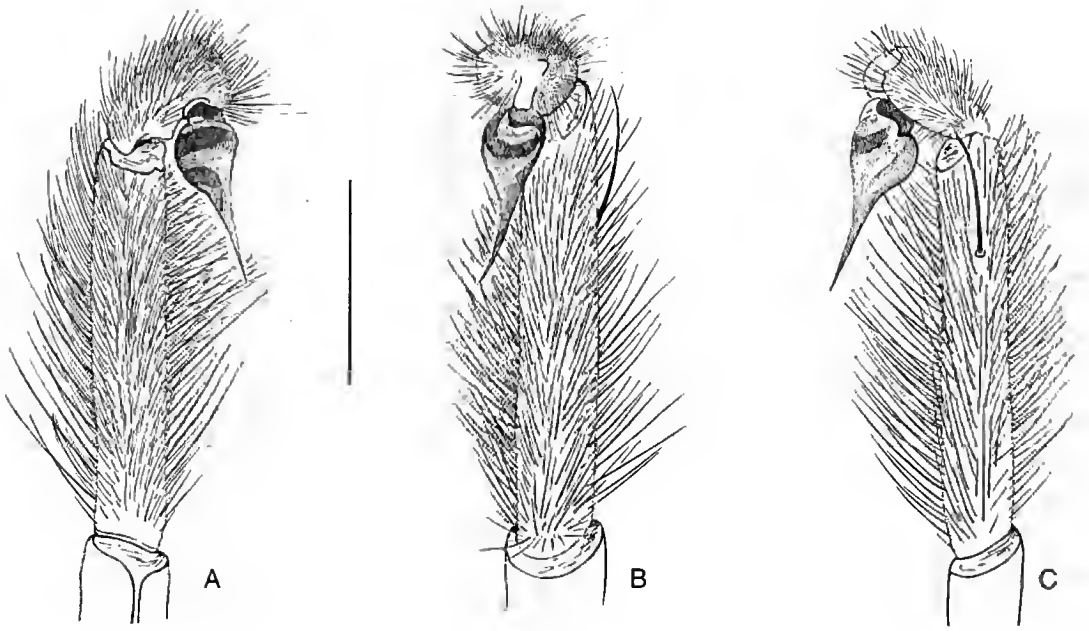


FIG. 4. — *Harmonicon audeae* n.sp., allotype ♂, pédipalpe droit. **A**, profil externe ; **B**, vue ventrale ; **C**, profil interne. Échelle : 3 mm.

rieures latérales longues et fines avec un article apical effilé.

Allotype mâle

Longueur totale sans les chélicères, 28 mm.

D'aspect plus grêle, le mâle diffère de la femelle par les points suivants :

Carapace. Longueur 13 mm ; largeur 10,5 mm.

Yeux. Yeux médians antérieurs proportionnellement plus gros que chez la femelle (Fig. 3A).

Chélicères. Marge interne avec onze dents coniques en ligne. Gouttière munie d'une simple série longitudinale de denticules ; plage de la partie basale présente, mais peu visible car non chitinisée comme chez la femelle (Fig. 3B).

Lames maxillaires. Serrula absente. Lyre identique.

Pédipalpe. Présence d'une épine prolatérale dans le tiers apical du tibia. Embolus piriforme terminé en courte pointe effilée (Fig. 4).

Pattes. Proportionnellement plus longues et fines avec des rapports ambulatoires qui varient de 3 à 3,5. Scopulas plus denses que chez la femelle. Présence, dans la partie apicale des tibias I, d'un éperon constitué d'un processus surmonté d'une forte épine (Fig. 3C, D).

Mensurations en mm	I	II	III	IV	Pd
Fémur	15,5	13,75	12,75	15	7,5
Patelle	6	5	5	5	3,25
Tibia	15	13	10,5	13,5	6,75
Métatarse	15	13,5	14,25	17	–
Tarse	9,25	8,75	7,25	8,5	2,5
Longueur totale	68,25	60,75	56	66	26
Diamètre fémur	2,15	2,1	1,85	2	–
Rapport ambulatoire	3,15	3,46	3,3	3,03	–

Filières. Longueur des postérieures médianes 2,75 mm. Longueur des postérieures latérales 21,5 mm ; article basal 5,5 mm ; article médian 6,5 mm ; article apical 9,5 mm. Pas de différence significative avec les filières de l'holotype femelle (Fig. 3E).

HABITAT

Harmonicon audeae, à l'instar de *H. rufescens,* est une Dipluridae forestière. Elle affectionne particulièrement la base des arbres, les souches ou les cavités naturelles des talus où elle tisse une toile en nappe horizontale munie d'un tube retraite qui s'enfonce profondément dans les anfractuosités du substrat. La partie plane de la construction soyeuse, soutenue par des fils verticaux, est largement étendue à l'extérieur et peut atteindre une superficie de près d'un mètre carré.

Obscuricole, *H. audeae* n'a jamais été vue de jour. Dès la tombée de la nuit, elle se poste à l'affût dans sa toile, tout près de l'entrée de son tube. D'une grande agilité, cette araignée est prompte à regagner sa retraite à la moindre alerte. Déjà noté par Pickard Cambridge (1896) pour *H. rufescens,* ce comportement rend sa capture difficile. Les mâles, errants, sont plus aisés à capturer, notamment à l'aide de pièges dits de Barber ou « *pit fall traps* ».

Selon les témoignages d'Amérindiens locaux, plus particulièrement des Oyampis, cette mygale serait très venimeuse. Toutefois, aucun cas d'envenimation n'est actuellement connu des services médicaux guyanais.

Remerciements

Tous mes remerciements vont au Dr P. Hillyard du Natural History Museum de Londres qui a bien voulu me confier le matériel-type nécessaire à l'élaboration de ce travail. Mes remerciements également à M. J. Rebière pour la réalisation des dessins de la figure 4.

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A new pedunculate cirripede (Thoracica, *Heteralepas*) from the Northeast Atlantic Ocean

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Carriol R.-P. 1998. — A new pedunculate cirripede (Thoracica, *Heteralepas*) from the Northeast Atlantic Ocean. *Zoosystema* 20 (3): 505-509.

KEY WORDS
Crustacea,
Cirripedia,
Thoracica,
taxonomy,
Meteor Seamount,
Northeast Atlantic.

ABSTRACT
A new species of *Heteralepas* is described from waters of 300 m at Meteor Seamount, south of the Azores, in the Northeast Atlantic Ocean. This species possesses a peduncle longer than the capitulum, a carinal crest without protuberances and continuing onto the peduncle, and it lacks scuta.

MOTS CLÉS
Crustacea,
Cirripedia,
Thoracica,
taxonomie,
banc Météor,
Atlantique (Nord-Est).

RÉSUMÉ
Un nouveau cirripède pédonculé (Thoracica, Heteralepas*) du nord-est de l'océan Atlantique.* Description d'une nouvelle espèce d'*Heteralepas* trouvée par 300 m de fond, sur le banc Météor, au sud des Açores, dans l'est de l'Atlantique nord. Cette espèce possède un pédoncule plus long que le capitulum et une crête carinale, sans protubérances, se prolongeant le long du pédoncule, mais n'a pas de scuta.

INTRODUCTION

The Meteor Seamount was sampled by the *Lesivy* during a trawling survey in August 1990. The expedition was sponsored by the FROM-Bretagne. M. H. Du Buit identified the fish fauna (Du Buit 1991) and provided the specimens of *Heteralepas* for study. This new taxon is the sixth species of *Heteralepas* from the Atlantic Ocean.

SYSTEMATICS

Subclass CIRRIPEDIA Burmeister, 1834
Superorder THORACICA Darwin, 1854
Order PEDUNCULATA Lamarck, 1818
Suborder HETERALEPADOMORPHA Newman, 1987
Family HETERALEPADIDAE Nilsson-Cantell, 1921

Genus *Heteralepas* Pilsbry, 1907

SPECIES INCLUDED. — The 21 taxa presently attributed to this genus include : *H. cornuta* (Darwin, 1851); *H. japonica* (Aurivillius, 1892); *H. lankesteri* (Gruvel, 1900); *H. belli* (Gruvel, 1902); *H. microstoma* (Gruvel, 1902); *H. gigas* (Annandale, 1905); *H. ovalis* (Hoek, 1907); *H. tenuis* (Hoek, 1907); *H. rex* (Pilsbry, 1907a); *H. cygnus* Pilsbry, 1907b; *H. nicobarica* Annandale, 1909; *H. vetula* Pilsbry, 1909; *H. dubia* Broch, 1922; *H. hataii* Hiro, 1937; *H. utinomii* Newman, 1960; *H. mystacophora* Newman, 1964; *H. luridas* Zevina, 1975; *H. adiposa* Zevina, 1982; *H. fulva* Zevina, 1982; *H. smilius* Ren, 1983; plus the new species described here: *Heteralepas meteorensis* n.sp.

DIAGNOSIS. — "Inner rami of cirri V and VI atrophied; articles of cirri (except cirrus I and inner rami of V and VI) rectangular; cirri long; lesser curvature of cirri supporting large pair of setae and one or two smaller pairs from the same origin; greater curvature supporting a few unpaired setae." (Newman 1960).

Heteralepas meteorensis n.sp.
(Fig. 1)

TYPE MATERIAL. — The types and additional specimens are deposited in two places, the Laboratoire de Zoologie-Arthropodes, Muséum national d'Histoire naturelle, Paris [holotype MNHN-Ci2689; paratypes MNHN-Ci2690 (specimen opened) and MNHN-Ci2691 (dissected, appendages preserved in alcohol); additional specimens MNHN-Ci2692 (1 specimen) and MNHN-Ci2693 (a small colony of about 15 adults] and the Laboratoire de Biologie marine du Collège de France, Concarneau [additional material (a colony of several tens of adults)].

ETYMOLOGY. — Named for the Meteor Seamount, the type locality.

TYPE LOCALITY. — Meteor Seamount, south of Azores Islands (30°N - 28°30'W), at 300 m depth, living on *Callogorgia* sp. (Alcyonaria).

DIAGNOSIS
Peduncle obviously longer than capitulum; capitulum lacking scuta; distinct carinal crest, without protuberances, continuing onto the peduncle.

DESCRIPTION
Specimens yellow pink in alcohol. Capitulum globular, laterally compressed, carinal margin broadly convex with carinal crest extending from orifice over the capitulum to the base of peduncule; scutal crest absent; lacking valves. Orifice between one fourth and one third height of capitulum; lips slightly crenulate. Peduncle long, annulated, two to four times length of capitulum (Table 1), cylindrical, with diameter equal to capitulum width.

TABLE 1. — Measurements (in cm) of capitulum and peduncle.

		Holotype MNHN-Ci2689	Paratype MNHN-Ci2690	Paratype MNHN-Ci2691
capitulum	height	1.6	1.8	1.2
	depth	1.4	1.7	1.2
	width	0.7	1	0.8
peduncle	length	3.4	7.2	3.1
	diameter	0.7	1-1.3	0.8

Labrum slightly bullate, anterior portion with tufts of short fine setae, crest with twenty-five small, sharp teeth; palps nearly triangular, superior margin with numerous long spines.
Mandible with four teeth including inferior angle, covered with short spinules; lower margin of first tooth with few spinules and some minute setae; lower margin of second and third teeth with several tiny spinules; upper margin of

second, third and fourth teeth with tiny spinules. Superior margin of mandible with tuft of long thin spinules and tuft of shorter spinules, inferior margin supporting row of numerous short thin spinules.

First maxilla notched; portion above notch with a single strong spine; notch supporting a long spine below and two long spines above with a short spine and two long thin spines between; lower cutting edge with long and some shorter spines; short spines in two groups along superior margin, tuft of few spinules near base of first major spine, brush of spinules along inferior margin; surface clothed with numerous spinules arranged in rows.

Second maxilla broadly rounded; distal portion with tufts and rows of long thin pinnate spinules; proximal portion with a tuft of very long pinnate spinules.

TABLE 2. — Number of articles of right cirri (I-VI) and caudal appendage (ca) from the paratype MNHN-Ci2691.

	I	II	III	IV	V	VI	ca
Inner ramus	19	59	77	87	23	26	14
Outer ramus	30	68	83	90	93	92	

Inner rami of cirri V and VI atrophied (Table 2). Lesser curvature of cirrus V supports one pair of long, one pair of short, and one pair of minute setae, from nearly common base on each segment. At base of long pair of setae, a very short

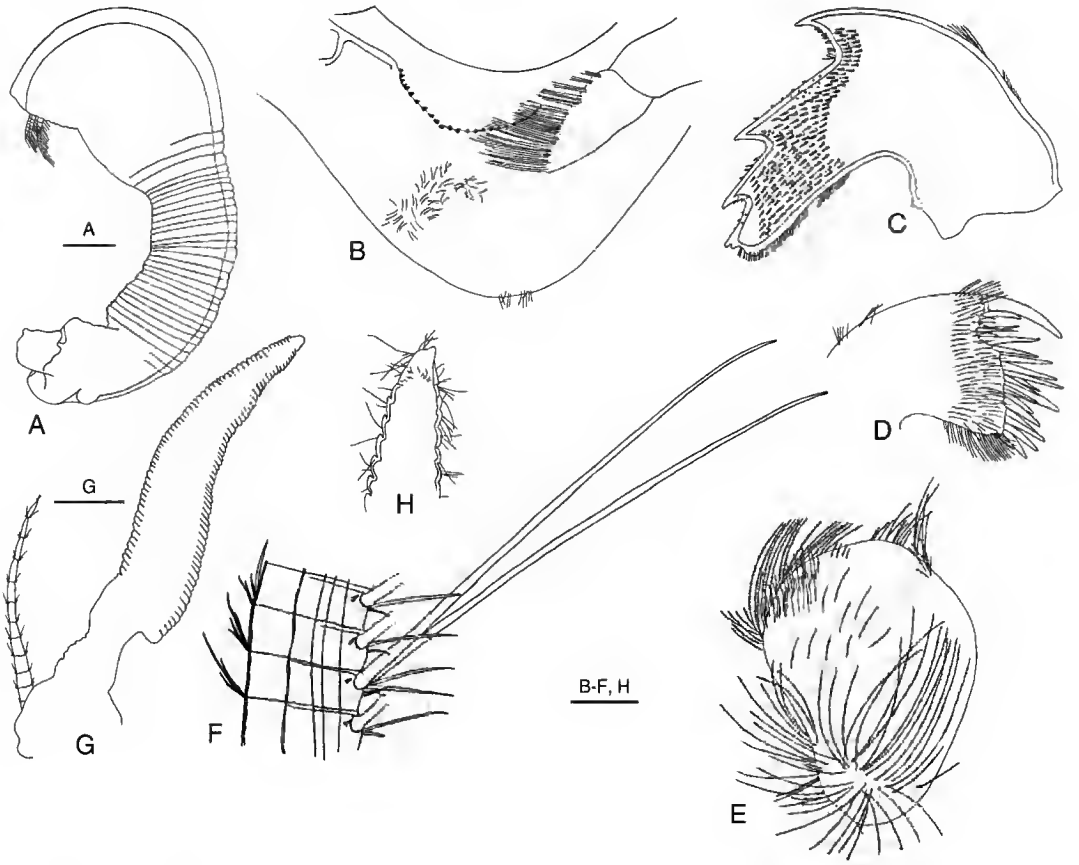

FIG. 1. — *Heteralepas meteorensis* n.sp.; **A**, holotype MNHN-Ci2690; **B-G**, paratype MNHN-Ci2691; **B**, labrum and right palp; **C**, mandible; **D**, first maxilla; **E**, second maxilla; **F**, intermediate article of outer ramus of cirrus V; **G**, penis and caudal appendage; **H**, distal part of penis. Scale bars: A, 4 mm; B-F, H, 0.5 mm; G, 1 mm.

TABLE 3. — Species of the genus *Heteralepas* of the world ocean.

Heteralepas	Western Atlantic	Eastern Atlantic	Eastern Pacific	Indo-Pacific
H. cornuta	West Indies, North Caroline	Western Africa	Chile	Adaman Sea, Philippines
H. japonica	–	–	–	Japan, China, Indo-Malaysian waters, Philippines, Australia, New Zealand
H. lankesteri	West Indies, Brazil	–	–	–
H. belli	Cuba	–	–	–
H. microstoma	–	Madera	–	–
H. gigas	–	–	–	Malaysia
H. ovalis	–	–	–	Malaysia
H. tenuis	–	–	–	New Guinea
H. rex	–	–	–	Hawaii
H. cygnus	–	–	California	–
H. nicobarica	–	–	–	Nicobar Islands
H. vetula	–	–	–	Japan
H. dubia	–	–	–	New Zealand
H. hataii	–	–	–	Japan
H. utinomii	–	–	–	Tasmania
H. mystacophora	–	–	Southeast Pacific	–
H. luridas	Carribbean	–	–	–
H. adiposa	–	–	–	Japan
H. fulva	–	–	Southeast Pacific	–
H. smilius	–	–	–	China
H. meteorensis n.sp.	–	South of Azores	–	–

spinule arises. Greater curvature supports graded series of three or four short setae at each articulation.

Caudal appendage of fourteen articles with thin setules at distal margins (Table 2).

Penis weakly annulated, slender, tapering gradually throughout its length; covered with numerous long, soft setae.

DISCUSSION

Zevina (1982) divides the *Heteralepas* in two groups: those with the peduncle obviously longer than the capitulum and those with the peduncle shorter. *Heteralepas meteorensis* n.sp. belongs to the first group. It differs from *H. gigas* by lacking scuta. The carinal crest without protuberances distinguishes *H. meteorensis* n.sp. from *H. fulva* and *H. nicobarica*. *H. meteorensis* n.sp. cannot be confused with *H. cygnus*, in which the carinal crest does not continue on the peduncle.

DISTRIBUTION

Heteralepas attains greatest diversity in the Indo-Pacific (Zevina 1982; Ren 1983; Rosell 1991): among the twenty-one species of which this genus consists (Table 3), sixteen are exclusively from Indian and Pacific Oceans and four are exclusively from Atlantic Ocean. Only one species, *H. cornuta*, is known from both the Atlantic and Pacific Oceans. *H. meteorensis* n.sp. is along with *H. microstoma* and *H. cornuta* (the latter two from Madera and Western Africa respectively). *H. cornuta* also occurs in Western Atlantic Ocean (West Indies, North Caroline) as does *H. luridas* (Caribbean), *H. lankesteri* (West Indies, Brazil) and *H. belli* (Cuba).

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A new species of the genus *Pasiphaea* from the South Indian Ocean (Crustacea, Decapoda, Pasiphaeidae)

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KEY WORDS
Pasiphaea gelasinus,
new species,
Pasiphaeidae,
Caridea,
Decapoda,
Crustacea,
South Indian Ocean.

ABSTRACT
Pasiphaea gelasinus n.sp. belongs to a group of *Pasiphaea* species characterized by a distally notched telson and a mid-dorsal carina on carapace and some or all abdominal segments. Within this group, it is distinguished by the rostral profile with anterior margin nearly vertical with a distinctive convexity, and by the presence of a distinct hollow laterally on the carapace on each side of the rostral base. The merus/ischium/basis spine formula for the first pereopod is 1-3/0/0 and for the second pereopod 7-12/0/0.

MOTS CLÉS
Pasiphaea gelasinus,
espèces nouvelles,
Pasiphaeidae,
Caridea,
Decapoda,
Crustacea,
océan Indien Sud.

RÉSUMÉ
Une nouvelle espèce du genre Pasiphaea *du sud de l'océan Indien. Pasiphaea gelasinus* n.sp. appartient à un groupe de *Pasiphaea* caractérisé par un telson terminé par une encoche et la présence d'une carène dorsale sur la carapace et sur quelques-uns ou tous les segments abdominaux. Dans ce groupe, cette espèce se distingue par le profil de son rostre dont le bord antérieur est presque vertical avec une convexité distincte et par la présence d'une dépression latérale nette sur la carapace, de chaque côté de la base du rostre. La formule donnant le nombre des épines sur le mérus, l'ischion et le basis des premiers péréiopodes est 1-3/0/0 et, pour les seconds, 7-12/0/0.

INTRODUCTION

Recently, the Muséum national d'Histoire naturelle, Paris, carried out, under the leadership of Guy Duhamel, an exploratory fishing cruise on the seamounts off Saint Paul and Amsterdam Islands. The area is interesting from the zoogeographical view point, but little systematic research has been done in the area so far. During the examination of pelagic shrimps collected from that area, we found an undescribed large species of the genus *Pasiphaea* Savigny, 1816. It is nearly 150 mm in total length and is characterized by the carinared carapace and abdomen, the armed meri of the first and second pereopods, and the deeply forked distal margin of the telson. An unusual dimple-like hollow is uniquely present on eirher side of the rostral base. All type material is preserved at the Muséum national d'Histoire naturelle, Paris.

ABBREVIATIONS

CL carapace length, measured in decapod shrimps from the orbit to the mid-dorsal point of the posterior margin of the carapace;
CP pelagic trawl;
MNHN Muséum national d'Histoire naturelle, Paris.

SYSTEMATICS

Genus *Pasiphaea* Savigny, 1816

Pasiphaea gelasinus n.sp.
(Figs 1-3)

MATERIAL EXAMINED. — **South Indian Ocean.** Seamounts off Saint Paul and Amsterdam Islands, research compaign 1996, CP 10, 37°37.8'S - 77°51.8'E, depth 730-905 m, 3.VII.1996: holotype ♂, CL 35.2 mm (MNHN-Na 13438); paratypes 1 ♂, CL 32.0 mm, 1 ♀, CL 34.0 mm (MNHN-Na 13439). — CP 6, 37°37.2'S - 77°55.5'E, depth 310-520 m, 3.VII.1996: paratype ♀, CL 22.0 mm (MNHN-Na 13460). — CP 12, 37°37.9'S - 77°51.7'E, depth 685-830 m, 4.VII.1996: paratypes 1 ♂, CL 36.0 mm, 2 ♀♀, CL 33.1, 49.5 mm (MNHN-Na 13459).

ETYMOLOGY. — The specific name *gelasinus* is Latin for "dimple" used as a nominative in apposition. The English word "dimple" (French "*fossette*") is a small natural dent or crease in the flesh, especially on the cheek or chin, or else a slight depression in any surface, and refers in this species to the dimple-like hollow on each side of the rostral base.

DISTRIBUTION. — Known only from the South Indian Ocean, near Saint Paul and Amsterdam Islands, at depths of 310-905 m.

SIZE. — The complete male selected as the holotype is CL 35.2 mm. The females are CL 22.0-49.5 mm. No ovigerous females are available, but the female of CL 33.1 mm shows many ovarian eggs through the carapace.

DIAGNOSIS

Shell firm. Rostrum continuous from dorsal margin of carapace, not reaching anterior margin of carapace. Carapace dorsally carinated; a distinct hollow at each side of rostral base; branchiosregal sinus small. All abdominal segments without terminal spine; first segment dorsally rounded; second to sixth segments dorsally carinated. Telson slightly shorter than sixrh segment; posterior margin deeply notched, with more than six pairs of spines. Firsr pereopod with one to three spines on merus; ischium unarmed; basis unarmed, posterodistal end rectangular with setae but sometimes acutely poinred; finger slightly shorter than palm. Second pereopod with ten to twelve spines on posterior margin of merus; unarmed on ischium; unarmed on basis excluding posterodisral spine; finger longer than palm. Ischium of third pereopod without spinules on posterior margin. Pleurobranch on eighth thoracic segment well-developed, as large as arthrobranch on sixth segment. Male holotype 35.2 mm in CL and largest female 49.5 mm in CL.

DESCRIPTION

Large pasiphaeid (Fig. 1). Rosrrum triangular in lateral view, but posterior (or upper) margin smoothly continuous with dorsal margin of carapace, anterior (or lower) margin nearly or obliquely vertical with slight convexity along entire margin, apex acute, pointed forward nearly reaching anterior margin of carapace (Fig. 2A). Carapace disrincrly carinated on dorsal margin from posterior margin of rostrum to posterior

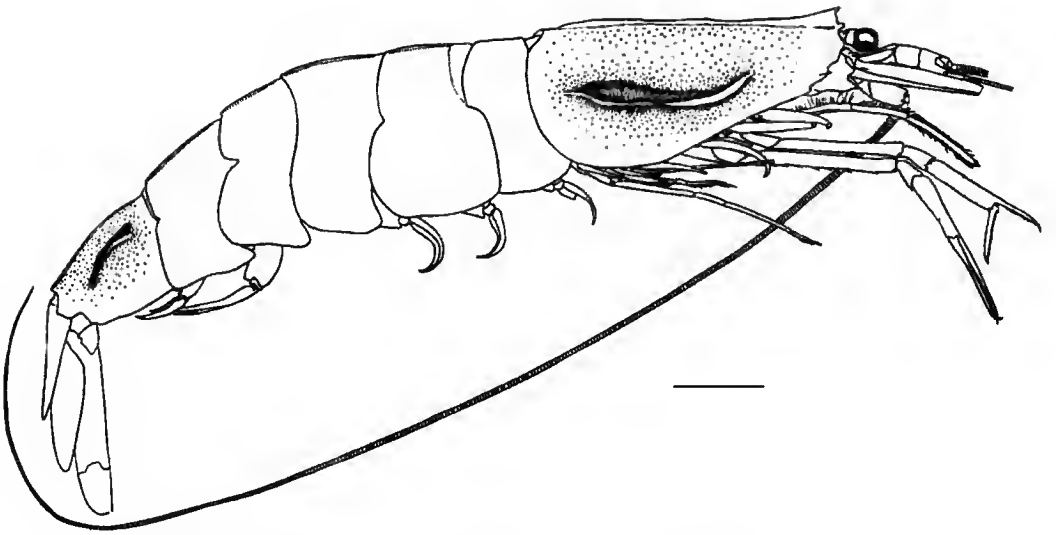

FIG. 1. — *Pasiphaea gelasinus* n.sp. Holotype ♂, CL 35.2 mm. Scale bar: 10 mm.

1/4-1/5 of carapace; distinct hepatic ridge continuous backward with branchiocardiac ridge, but ill-defined posteriorly; shallowly depressed around rostral base and with a distinct hollow laterally along each side of rostral base (Fig. 2A, B). Branchiostegal spine arising just inside anterolateral margin of carapace, not supported by carina; apex overreaching anterior margin (Fig. 2A). Branchiostegal sinus small but distinct (Fig. 2A).

Only three specimens including holotype with distal part of abdomen. First abdominal segment rounded dorsally. Second to fifth segments with distinct dorsal carina (Fig. 2C). Sixth segment compressed, 1.3-1.4 times as long as fifth segment and about 1.3-1.5 times as long as deep (Fig. 2D); dorsal margin sharply carinated on anterior two thirds, and flattened on posterior third; from lateral view, posterior end somewhat produced posteriorly and dorsal margin before posterior end slightly depressed (Fig. 2D). Telson 0.8-0.9 times as long as sixth segment, dorsally grooved for entire length (Fig. 2E); distal margin deeply forked, distal end not complete in all specimens, but at least ten spines recognizable on one side in one specimen (Fig. 2F).

Eye well-developed; cornea larger than eyestalk; from dorsal view, cornea and eyestalk obliquely divided into two equal parts (Fig. 2G). Stylocerite nearly reaching end of first antennular segment; upper distal end small and spiniform, directed obliquely upward (Fig. 2A). Antennal scale 3.9-4.0 times as long as wide (Fig. 2H), and as long as or slightly longer (1.0-1.1) than first chela and a little shorter (0.85-0.95) than second chela (Fig. 1); basicerite with medium-sized spine on lower distal corner (Fig. 2A). Mouthparts of typical shape for genus (Fig. 3A-G). Endopod of first maxilliped small process with single seta (Fig. 3E).

Posterodistal corner of basis of first pereopod rectangular with seta, not forming typical spine but sometimes ending in acute point; ischium unarmed; merus with one to three spines on distal half of posterior margin; chela of typical shape, finger shorter (46-47% of chela) than palm; series of more than ten spinules on lower mesial margin of palm to base of immovable finger (Fig. 3H). Basis of second pereopod ending in distinct spine, unarmed on posterior margin; ischium unarmed on posterior margin; merus with seven to twelve spines on posterior margin; palm shorter (39-43% of chela) than fingers and as long as or slightly shorter than that of first (Fig. 3I). No spinules on ischium of third pereopod (Fig. 3J). Fourth and fifth pereopods of typical shape for genus (Fig. 3K, L).

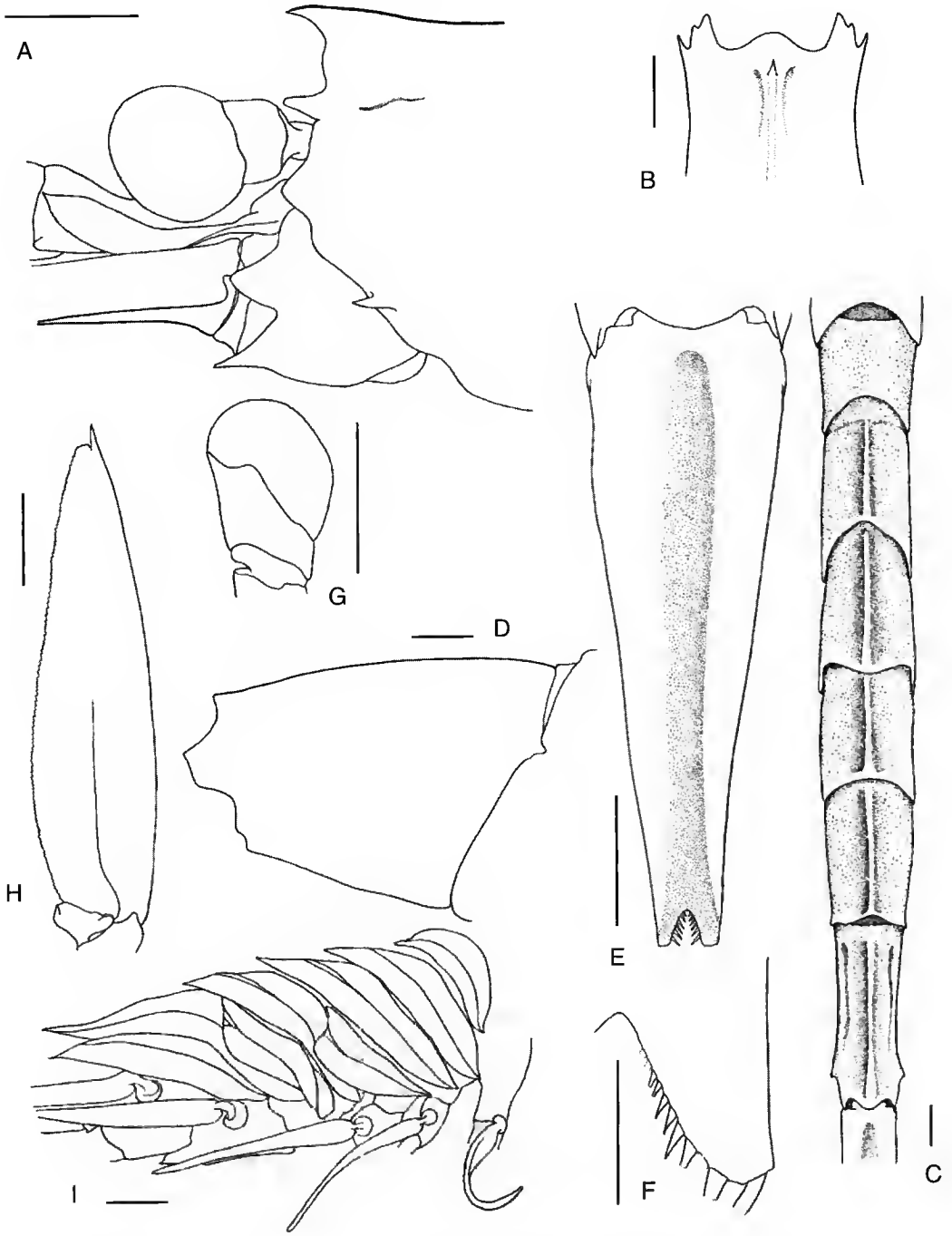

FIG. 2. — *Pasiphaea gelasinus* n.sp; **A**, F, paratype ♀, CL 33.1 mm; **B-E**, **G**, holotype ♂, CL 35.2 mm; **H**, paratype ♂, 32.1 mm; **I**, paratype ♀, 34.0 mm; **A**, anterior part of body in lateral view; **B**, anterior part of carapace in dorsal view; **C**, abdomen in dorsal view; **D**, sixth abdominal segment in lateral view; **E**, telson in dorsal view; **F**, telson end in dorsal view; **G**, eye in dorsal view; **H**, antennal sale in dorsal view; **I**, left gill chamber, from left to right first to fifth pereopods. Scale bars: A-E, G-I, 3 mm; F, 1 mm.

Endopod of male first pleopod composed of two lobes, mesial lobe small, with many retinaculae in central part; outer lobe large, surrounded by many long plumose setae (Fig. 3M). Endopod of male second pleopod of typical shape for genus; appendix masculina with several long setae, not reaching end of appendix interna (Fig. 3N).

Branchial formula as follows :

	Maxillipeds		
	First	Second	Third
Pleurobranchs	–	–	–
Arthrobranchs	–	–	–
Podobranchs	–	–	–
Epipods	–	–	–
Exopods	–	–	1

	Pereopods				
	First	Second	Third	Fourth	Fifth
Pleurobranchs	1	1	1	1	1
Arthrobranchs	1	1	1	–	–
Podobranchs	–	–	–	–	–
Epipods	–	–	–	–	–
Exopods	1	1	1	1	1

REMARKS

The more than sixty species in the genus *Pasiphaea* Savigny, 1816 (Burukovsky 1996) can be divided into a number of groups of species based on charactets of the telson, carapace, abdomen and first two pereopods. The present new species belongs to a species group which is characterized by a deeply forked telson end, by a dorsally carinated carapace and abdomen, and by the armed meri of the first and second pereopods. The distal margin of the telson must be clearly notched, not just weakly concave. The carapace carina may not necessarily extend all the way from the rostral blade to the posterior dorsal margin of the carapace but it must extend posteriorly from the rostrum along a considerable proportion of the dorsal surface. The carapace dorsal carination may not necessarily be sharp and blade-like, it may be somewhat rounded, but it must appear as a distinct dorsal carination. All abdominal segments need not be carinated but at least most of the third, the fourth, the fifth and at least the anterior part of the sixth abdominal segments must be carinated. Once again the abdominal dorsal segmental carination need not all be sharp and blade-like, but the segments must be clearly carinated. The sharpness of the carapace and abdominal dorsal carination, if present, in the genus *Pasiphaea* appears, at least in some species, to be related to size, age, and position in molt cycle of the individual specimen. The number of meral spines on the first and second pereopods varies considerably with growth or size, but the presence or absence, many or a few in number, and their position, if present, are good specific characters.

The present group in the genus *Pasiphaea* includes the following twelve nominate species listed in alphabetical order:
P. acutifrons Bate, 1888;
P. alcocki (Wood Mason, 1891) *in* Wood Mason & Alcock (1891);
P. balssi Burukovsky *et* Romensky, 1987;
P. barnardi Yaldwyn, 1971 (synonyms *P. meiringnaudei* Kensley, 1977; *P. berentsae* Kensley *et al.*, 1987);
P. faxoni Rathbun, 1902;
P. grandicula Burukovsky, 1976;
P. korzuni Burukovsky, 1995;
P. multidentata Esmark, 1866;
P. pacifica Rathbun, 1902;
P. rathbunae (Stebbing, 1914);
P. sinensis Hayashi *et* Miyake, 1971;
P. tarda Krøyer, 1845 (synonym *P. principalis* Sund, 1913).

Within this group, two species can be immediately separated from *P. gelasinus* as follows: in *P. alcocki*, the first to fifth segments of abdomen are dorsally smooth and only the sixth segment is dorsally carinated (Wood Mason 1893); in *P. pacifica*, the branchiostegal spine is placed on the side of the carapace, more or less above the branchiostegal sinus, well inside the anterolateral margin of the carapace and not extending anywhere near the anterolateral margin, and the merus of the first pereopod is usually unarmed but up to four spines are present on some specimens (Rathbun 1902; 1904; Butler 1980).
Seven further species of this group can be

separated from *P. gelasinus* as their second pereopods are spined on the basis and often on the ischium, as well as on the merus: in *P. balssi* the merus/ischium/basis spine formula for the second pereopod is 16-19/1-2/10-16 (rostrum extending well beyond front of carapace) (Burukovsky & Romensky 1987); *P. barnardi* second pereopod spine formula, 7-21/0-2/1-7, though some small specimens may have one or both second pereopod bases unarmed (rostrum extends to just beyond front of carapace) (Yaldwyn 1971; Burukovsky 1978; Kensley 1977 as *P. meiringnaudei*; Kensley *et al.* 1987 as *P. berentsae*); *P. grandicula* second pereopod spine formula, 11-44/2-5/6-41, number of spines increasing with size (rostrum extending beyond front of carapace) (Burukovsky 1976); *P. multidentata* second pereopod spine formula, 9-37/0-3/4-16 (rostrum narrow and acute, reaching beyond front of carapace) (Esmark 1866; Sivertsen & Holthuis 1956; Zariquiey 1957, 1968); *P. rathbunae* second pereopod spine formula, 7-17/2/3-8 (branchiostegal spine arising from margin of carapace posterior to branchiostegal sinus) (Stebbing 1914; Hale 1941); *P. tarda* second pereopod spine formula, 12-22/0-1/1-9 (rostrum extending well beyond front of carapace and in mature specimens with a characteristic convex bulge on lower border of rostrum more or less above front of carapace) (Krøyer 1845; Sund 1913 as *P. principalis*; Sivertsen & Holthuis 1956; Butler 1980; Hayashi 1990).

P. gelasinus is similar to the remaining four species of this group in having the ischium and basis of the first and second pereopods unarmed. *P. gelasinus* has an acute rostrum, not extending beyond the front of the carapace, with a distinctive convexity on the nearly vertical lower margin of the rostrum in lateral view. *P. acutifrons*, *P. faxoni* and *P. korzuni* have rather similar rostral profiles, acute, usually not extending beyond front of carapace but without a nearly vertical lower margin with or without a distinctive convexity. *P. sinensis* has a rostral profile rather different from that of *P. gelasinus*, in having the lower margin with a convexity on midlength, extending beyond rostral apex and usually with a small concavity at base of lower margin.

P. gelasinus has a distinct hollow laterally on the carapace at either side of the rostral base (the "dimple" of its specific name). Neither *P. acutifrons*, *P. faxoni*, *P. korzuni* nor *P. sinensis* show this feature and, as far as we are aware, this feature is unique to *P. gelasinus* among described species of the genus *Pasiphaea*, though a similar hollow may be shown in figures of *P. diaphana* Burukovsky *et* Romensky, 1980 (Burukovsky 1993, fig. 2.1, 2.3). Such a hollow on the carapace is not mentioned in the original 1980 description of *P. diaphana*, nor is it shown in the earlier figures of this species published by Burukovsky & Romensky (1979, figs 1, 2) under the name *Pasiphaea flagellata* non Rathbun. *P. diaphana* belongs to the *Pasiphaea* species group characterized by a distally truncate telson, a non-carinated carapace and non-carinated abdominal segments, but with meri of first and second pereopods armed.

P. gelasinus has the merus of the first pereopod with one to three spines, and the merus of the second pereopod with seven to twelve spines. The four species of this group discussed in the last two paragraphs have first and second pereopod meral spines (based on published and unpublished information available) compared to those of *P. gelasinus* as follows:

	First pereopod Meral spines	Second pereopod Meral spines
P. gelasinus	1-3	7-12
P. acutifrons	1-8	10-32
P. faxoni	3-6	9-18
P. korzuni	1-5	11-20
P. sinensis	6-12	19-25

The closest species to *P. gelasinus* in this group would appear to be *P. sinensis* at nearly the same size, and with the abdomen also carinated on second to fifth, and anterior two thirds of sixth, segments. The lack of carapace hollows on either side of the rostrum, the dissimilar rostral profile, and the higher meral spine counts on both first and second pereopods in *P. sinensis* would appear to distinguish these two species on careful examination.

Although missing the posterior part of the abdomen, the smallest specimen of *P. gelasinus*

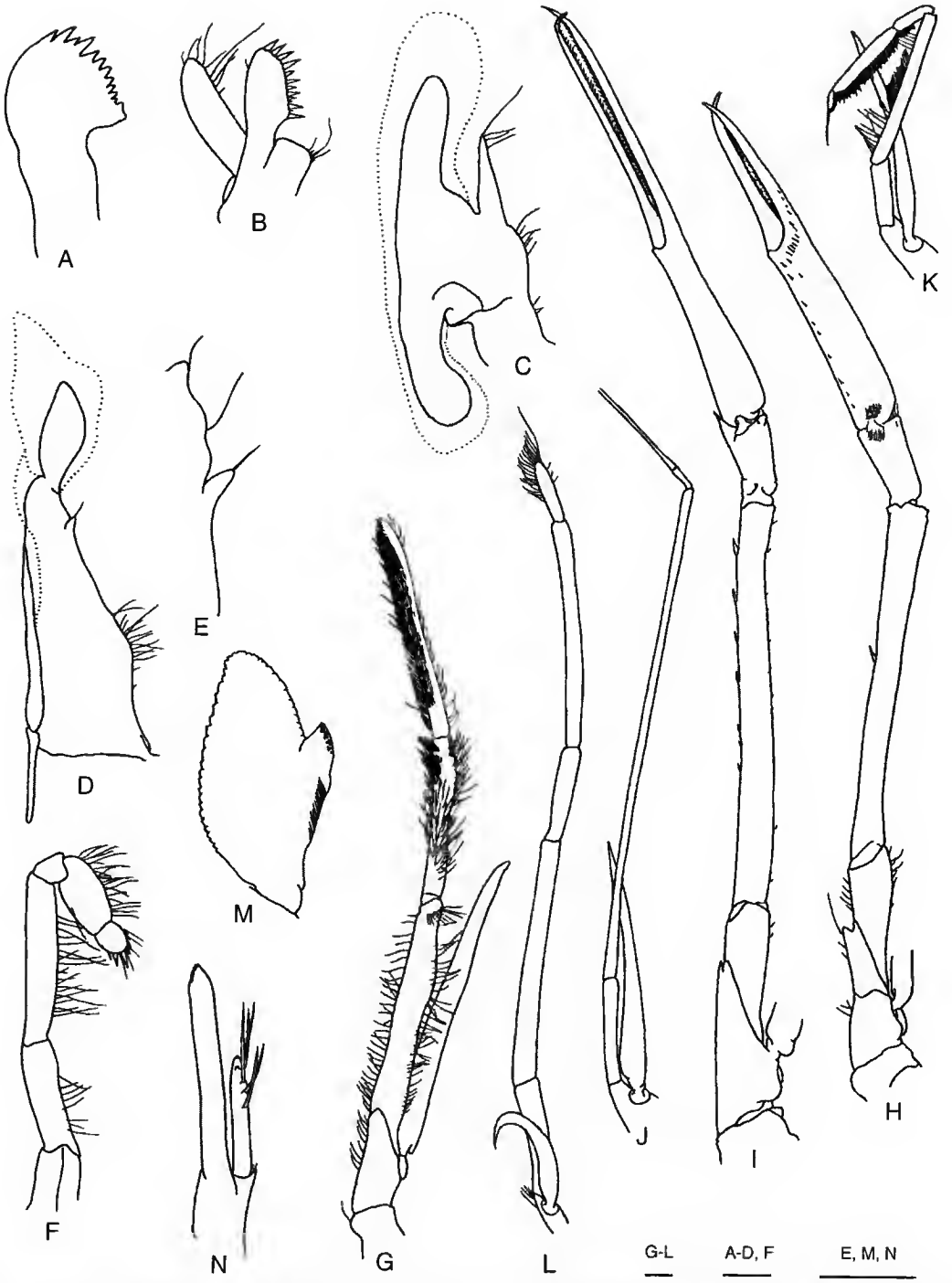

FIG. 3. — *Pasiphaea gelasinus* n.sp.; **A-I**, **M-N**, paratype ♂, CL 32.1 mm; **J-L**, paratype ♀, CL 34.0 mm; **A**, mandible; **B**, first maxilla; **C**, second maxilla; **D**, first maxilliped; **E**, end of first maxilliped; **F**, second maxilliped; **G**, third maxilliped, mesial view; **H**, first pereopod, mesial view; **I**, second pereopod, mesial view; **J**, third pereopod, outer view; **K**, fourth pereopod, outer view; **L**, fifth pereopod, outer view; **M**, end of first pleopod; **N**, appendices interna and masculina. Scale bars: 1 mm.

examined differs from the other larger specimens in having a slightly different shape and proportion; the dorsal margins of the remaining first and second segments are smooth with no trace of a carina, the eyes are comparatively longer as are the fingers of the second pereopod. These differences are probably due to the immaturity of the specimen.

The authors are aware of some giant specimens of *Pasiphaea* with CL up to 85 mm from the Tasman Sea, from off eastern Australia and from southern waters of Western Australia, under study in Japan and New Zealand, that are very similar in many features to *P. gelasinus*, and may or may not prove to be conspecific. The large specimens at least have a deep and anteriorly open furrow on the carapace each side of the rostrum, a carinated carapace and abdomen, and a distally notched telson. The specific status of these specimens (more than one species may be involved) is as yet undecided.

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Onychiuridae (Insecta, Collembola) d'Herzégovine en région karstique avec description d'une nouvelle espèce

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MOTS CLÉS
collemboles,
Onychiuridae,
systématique,
région karstique,
Herzégovine,
Europe.

RÉSUMÉ
L'étude des Onychiuridae (Insecta, Collembola) de deux massifs calcaires dominant le site de Medjugorje a conduit à la description d'une nouvelle espèce : *Hymenaphorura nicolae* n.sp. Celle-ci se caracrérise par un organe postantennaire prolongé dorsalement sur la tête, des macrochètes nettement différenciés sur le corps ; le tergite abdominal V porte 3 + 3 macrochètes, griffe sans dent interne. De plus, les genres *Doutnacia* et *Fissuraphorura* sont cités pour la première fois dans cette région.

KEY WORDS
Collembola,
Onychiuridae,
systematics,
karstic mountains,
Herzegovina,
Europe.

ABSTRACT
Onychiuridae (Insecta, Collembola) from Herzegovina with description of a new species from a karstic area. This paper deals with study of a new species *Hymenaphorura nicolae* n.sp. collected in two karstic mountains near Medjugorje (Herzegovina). This species is caracterized by an elongared posr-antennal organ, well differentiatied macrochetae on thoracic and abdominal segments ; tergire abdominal V has 3 + 3 macrochaetae and internal teethless claw. Moreover, the genera *Doutnacia* and *Fissuraphorura* are cited for the first time from this area.

INTRODUCTION

Les travaux sur la faune collembologique de Yougoslavie nous donnent une bonne connaissance de ce groupe (*cf.* Dunger & Zivadinovic 1989 pour la bibliographie). Les catalogues dressés témoignent de la répartition des espèces à travers les différentes régions du pays. La province d'Herzégovine et plus spécialement les massifs calcaires à climat chaud et sec semblent moins bien connus. Les collemboles Onychiuridae décrits ou cités dans cette note proviennent de deux massifs calcaires qui dominent le site de Medjugorje (Barra 1993). Les récoltes ont été faites au printemps (mai 1991) et en automne (octobre 1994, 1995 et 1997). Tous les échantillons ont été extraits à sec.

ABRÉVIATIONS

a0	soie médiane antérieure
c	soies de l'avant-dernière rangée postérieure
g	soies latéro-postérieures
oc	soies centro-latérales
p1-5	soies de la rangée postérieure
sd	soies parallèles à la série paramédiane d

SYSTÉMATIQUE

Hymenaphorura nicolae n.sp.
(Fig. 1A-K)

MATÉRIEL-TYPE. — Holotype ♂ et 4 paratypes (3 ♀♀ et 1 ♂) plus 7 paratypes juvéniles de 1 mm de longueur). L'holotype, un paratype ♀ et 2 paratypes juvéniles ont été déposés au Muséum narional d'Histoire naturelle, Paris.

LOCALITÉ-TYPE. — Medjugorje, massif du Podbrdo (altitude 400 m), sol brun léger couvert de lichens blanchâtres, le 8.X.1995. Station de récolte : Med. 17.

ÉTYMOLOGIE. — Espèce dédiée à mon épouse qui a récolté ce matériel.

DIAGNOSE

Gouttière de l'organe postantennaire prolongée dorsalement sur la tête. Grains tégumentaires distincts. Chétotaxie asymétrique, macrochètes distincts. Sur les tergites abdominaux de I à IV p2 plus petits que p3, sur abdomen V : 3 + 3 macrochètes. Griffe sans dent interne.

DESCRIPTION

Longueur totale : 1,9 mm. Coloration blanche. Les grains tégumentaires sont bien marqués sur toute la face dorsale et nettement plus développés sur le dernier segment abdominal (2,5-4 µm). Sur les antennes et sur la tête, ceux-ci mesurent entre 1,7-2 µm, sur les tergites : 2-2,5 µm. Les grains autour des pseudocelles et ceux qui les avoisinent atteignent 2,5 µm et jusqu'à 3,5 µm sur l'abdomen V ; ces grains forment des amas plus denses en relation avec leur structure et leur hauteur (Fig. 1E, F).

Antennes légèrement inférieures à la diagonale céphalique. Article antennaire IV avec des soies ordinaires, sans vésicule apicale, avec une microsensille subapicale et une seconde au tiers inférieur au-dessus de l'organe antennaire III (Fig. 1B). L'organe sensoriel d'antennaire III est constitué par deux masses allongées granuleuses et deux sensilles rectilignes ; cinq papilles tégumentaires coniques les protègent ainsi que quatre longues soies (Fig. 1B). Les papilles sont bosselées, exceptionnellement l'une d'elle peut-être bifide (Fig. 1C).

L'organe postantennaire en position latéroventrale est formé de douze à quatorze vésicules parallèles (Fig. 1D). La dépression profonde qui contient les vésicules se prolonge dorsalement sur la tête en s'incurvant vers l'arrière (Fig. 1A).

Les macrochètes dorsaux sont bien distincts. La formule des pseudocelles dorsaux par demi-tergite est : 10/011/11112 ; les pseudocelles vestigaux mal visibles ne peuvent être localisés avec certitude. Autour de chaque pseudocelle on dénombre dix à douze à 12 grains tégumentaires. Sur les aires denses circonscrites aux pseudocelles du corps, les soies p2 sont inférieures à p3, rapport p3/p2 = 1,2-1,4 sauf sur l'abdomen IV où p3/p2 = 2,3. Le tergite abdominal V porte 3 + 3 macrochètes (a4, p2, p5), a1 sont mésochètes comme p1 et p3, rapport : p1/a1 = 1, p2/a1 = 2,3. Abdomen VI avec deux épines anales, chaque épine est insérée sur une papille à trois couronnes de grains tégumentaires ; épines + couronnes égales aux griffes (Fig. 1I).

Les sternites thoraciques de I à III portent normalement 0, 1, 1 paires de soies, mais les combinaisons suivantes sont fréquentes : 0, 1 + 2, 1 + 2, voire 0, 2 + 2, 2 + 2, les juvéniles de 1 mm

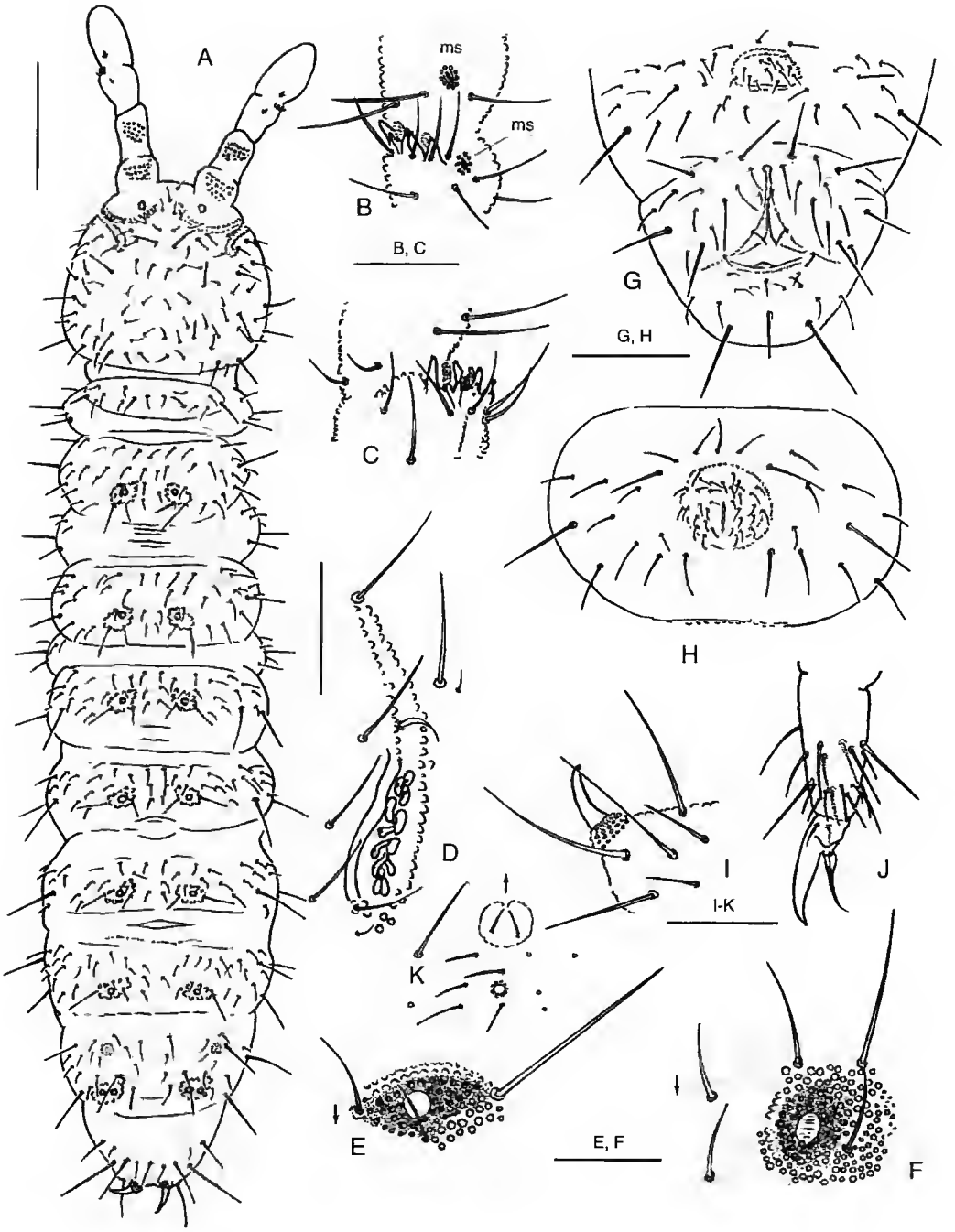

FIG. 1. — *Hymenaphorura nicolae* n.sp. ; **A**, chétotaxie dorsale et répartition des pseudopores ; **B**, organe antennaire III et microsensilles (ms) latéro-ventrales ; **C**, organe antennaire III avec une papille bifide ; **D**, organe postantennaire ; **E**, granulation autour du pseudocelle sur l'abdomen IV ; **F**, granulation autour du pseudocelle du thorax II ; **G**, papille génitale femelle ; **H**, papille génitale mâle ; **I**, épine anale ; **J**, tibiotarse III et griffe ; **K**, sternite IV : aire furcale, Ps : pseudopore. Échelles : A, 200 µm ; B, C, 40 µm ; D, 30 µm ; E, F, 27 µm ; G, H, 100 µm ; I-K, 30 µm.

de longueur n'ont pas encore de soies sternales. Pas de furca. Tube ventral avec 10-11 + 10-11 soies. Plaque génitale femelle avec dix à quatorze soies (Fig. 1G), plaque génitale mâle : 16 + 16 soies (Fig. 1H), organe ventral mâle absent.
Tibiotarses sans soies particulières, de I à III on dénombre 20, 20, 19 soies. Griffes sans dent interne. Empodium terminé en aiguille avec une courte lamelle basale, empodium égal ou légèrement inférieur à la griffe (Fig. 1J). À l'emplacement de la furca, on note dans les deux sexes une aire à granulations fines avec deux soies, en arrière et entre les deux macrochètes latéraux huit à neuf soies manubriales disposées le plus souvent d'une manière irrégulière (Fig. 1K). Sur la ligne médiane des sternites II à IV, on peut observer un pseudopore atypique par segment (observation non constante).

VARIABILITÉ
La chétotaxie dorsale n'est pas symétrique : perte de soies ou soies en surnombre. Les pseudocelles peuvent faire défaut d'un seul côté ou des deux côtés. La deuxième papille externe de l'organe antennaire III peut être fourchue (deux observations, mâle et femelle). Les griffes sont normalement sans dent interne, mais deux exemplaires présentaient une minuscule dent interne. À signaler aussi la variabilité des soies sternales thoraciques.

DISCUSSION
Les espèces d'*Hymenaphorura* du « groupe *sibirica* » ont été redéfinies et discutées par Pomorski (1990b). Sur la base de ce travail, Arbea & Jordana (1994) ont reconnu deux nouvelles espèces de la péninsule Ibérique. *Hymenaphorura nicolae* n.sp. répond aux critères définis par Pomorski. La répartition des zones à grains forts et contrastés place cette nouvelle espèce dans le type « A » (*sensu* Arbea & Jordana). Les soies p2 sont inférieures à p3 sur les tergites thoraciques et abdominaux comme chez *H. creatricis* Pomorski, 1990, mais cette dernière a toujours une dent à la griffe et 4 + 4 macrochètes sur l'abdomen V (a1, a4, p2 et p5), alors que *H. nicolae* n'en comporte que 3 + 3 (a4, p2 et p5). L'une des papilles de l'organe antennaire III est occasionnellement fourchue ; ce caractère, non lié au sexe, se retrouve exceptionnellement aussi chez *H. rea* Christiansen *et* Bellinger, 1980 et, d'une manière plus constante, chez *H. nova* Pomorski, 1990.

Les autres Onychiuridae rencontrés sur ces deux massifs calcaires sont :

Protaphorura du groupe ***fimata*** (Gisin, 1952)

LOCALITÉ. — Les onze exemplaires proviennent tous du même prélèvement Med. 02, récolté le 6.V.1991. Medjugorje : colline du Podbrdo (altitude 400 m). Petit massif couvert d'arbustes et d'épineux, laissant ça et là des plages dénudées, sol argileux rouge entre les blocs rocheux. Échantillon de sol (0 à –5 cm de profondeur) contre un rocher, J.-A. Barra leg.

Deux adultes des deux sexes et neuf juvéniles. Les pseudocelles dorsaux par demi-tergites sont répartis en 33/022/33333. Tous les caractères concordent avec les descriptions de Pomorski (1986 et 1990a).

Mesaphorura critica Ellis, 1976

LOCALITÉ. — Espèce présente dans tous les prélèvements de sol argileux sur les deux massifs calcaires proches de la ville de Medjugorje, la colline du Podbrdo et le Mont Krizevac (altitude 520 m). Récoltés en mai 1991 et octobre 1995.

Metaphorura affinis (Börner, 1902)

LOCALITÉ. — Espèce assez fréquente dans les prélèvements de sol argileux sur la colline du Podbrdo, à tous les niveaux. Récoltés en mai 1991 et octobre 1997.

Tous les exemplaires rencontrés correspondent à *M. affinis*, forme B selon Ellis, 1976 avec, comme formule pseudocellaire dorsale par demi-tergite, 11/111/11111. Parmi les seize exemplaires montés, sept présentent un organe postantennaire avec des vésicules bifides inégales. Comme le font remarquer Arbea & Jordana 1991, la reconnaissance de *M. bipartita* ne sera possible qu'en étudiant le matériel-type ou en utilisant le microscope électronique à balayage.

Metaphorura denisi Simon, 1985

LOCALITÉ. — Espèce plus rare, a toujours été trouvée

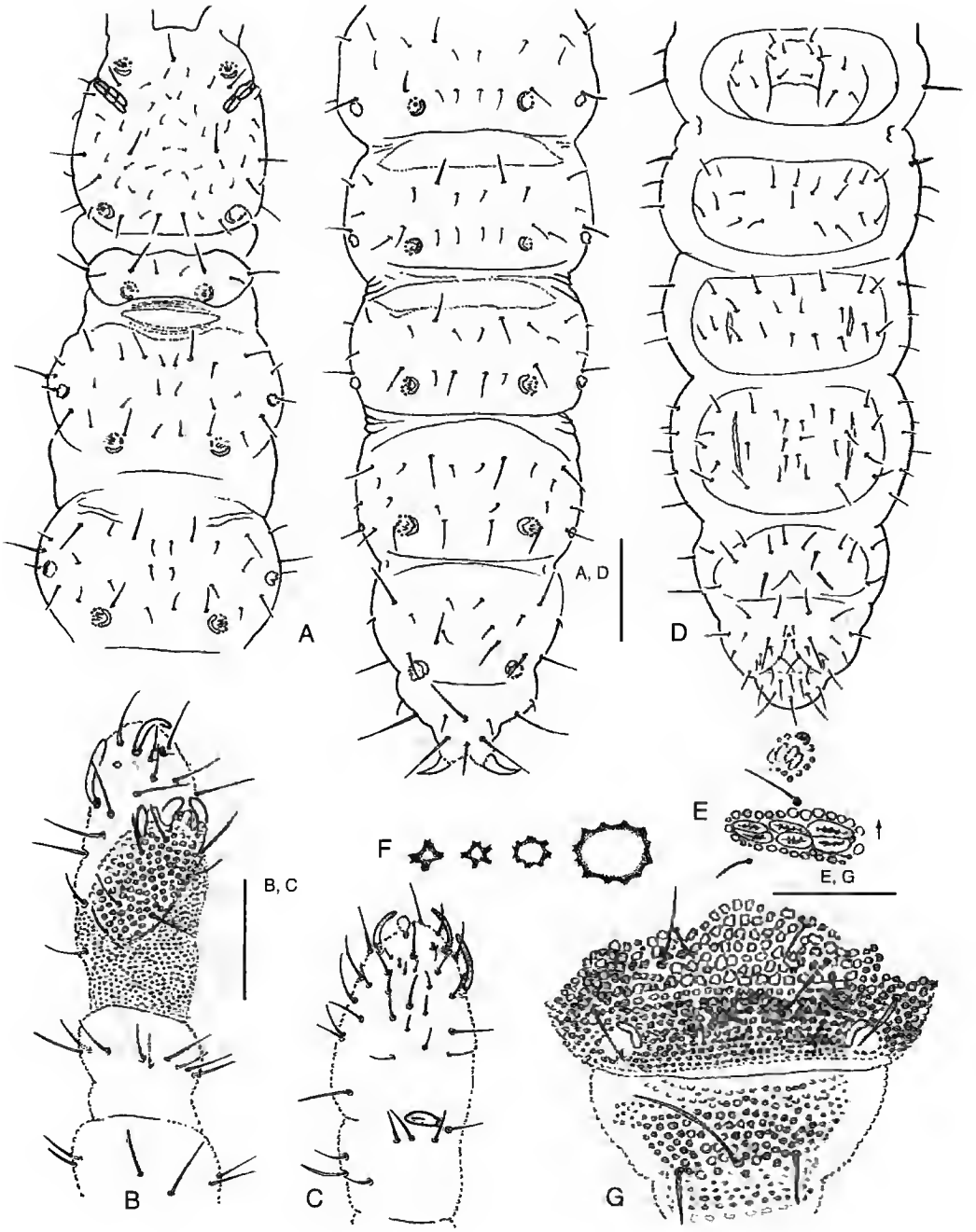

FIG. 2. — *Fissuraphorura* sp. ; **A**, chétotaxie dorsale ; **B**, antenne droite, face dorsale ; **C**, articles antennaires III et IV face ventrale ; **D**, chétotaxie des sternites abdominaux ; **E**, organe postantennaire ; **F**, aspect des grains tégumentaires sur les tergites abdominaux IV et V, 0,8 à 3,4 µm ; **G**, disposition des grains polygonaux sur l'abdomen V et VI. Échelles : A, D, 65 µm ; B, C, E, G : 30 µm.

Tableau 1. — Tableau comparatif des soies céphaliques des différentes espèces de *Fissuraphorura* (selon les dessins ou les données des auteurs). **M**, macrochètes ; **m**, mésochètes ; **µ**, microchètes.

Soies	*F. cubanica* Rusek, 1991	*F. deharvengi* Rusek, 1991	*F. duplex* (Gama, 1962)	*F. gisini* (Selga, 1963)	*F. miscellanea* Barra, 1995	*Fissuraphorura* sp.
a0	µ	m	M	m	M	M
sd4	µ	m	m	m	M	m
oc2	M	M	M	M	M	m
v1	µ	µ	µ	µ	µ	µ
v2	µ	µ	µ	µ	µ	µ
c5	M	µ	M	m	M	M
p1	µ	m	m	m	m	m
p3	µ	m	m	m	m	m
p5	M	M	M	M	M	M
g3	M	M	M	M	M	M

en compagnie de *M. affinis*. Cinq exemplaires récoltés en mai 1991 et une dizaine en octobre 1997 sur la colline du Podbrdo.

Cinq spécimens femelles ou immatures présentent, par demi-tergite, la formule pseudocellaire dorsale suivante : 11/122/22221. Selon Simon (1985), la forme C de Ellis (1976) se réfère à *M. denisi*.

Doutnacia xerophila Rusek, 1974

LOCALITÉ. — Espèce récoltée en nombre sur les deux massifs calcaires et dans tous les échantillons de sol en mai 1991 et octobre 1994, 1995, 1997.

Espèce très commune, présente dans tous les prélèvements en nombre variable.

Fissuraphorura sp.
(Fig. 2A-G)

MATERIEL ÉTUDIÉ. — Un seul exemplaire non adulte déposé au Laboratoire d'Entomologie du Muséum national d'Histoire naturelle, Paris.

LOCALITÉ. — Medjugorje, colline du Podbrdo (altitude 400 m). Petit massif couvert d'arbustes et d'épineux, laissant çà et là des plages dénudées à sol argileux rouge entre les blocs rocheux. Dans sol argileux (0 à −5 cm de profondeur) contre un rocher, le 6.V.1991. Extraction à sec. Station de récolte : Med. 2 ; J.-A. Barra leg.

DESCRIPTION

Taille : 0,95 mm. Coloration blanche. Le grain tégumentaire est bien marqué, dessinant une sorte de pavage à éléments polygonaux (Fig. 2G) sur la face dorsale de la tête, du corps et sur les articles antennaires III et IV. Sur le thorax et les segments abdominaux I et II, les grains mesurent 1,7 µm, sur l'abdomen III à V, 2,5 à 3,4 µm, sur le dernier segment abdominal ceux-ci atteignent 2,5 µm, mais sont nettement arrondis. Les grains résultent de la fusion de plusieurs grains primaires avec un halo clair au centre (Fig. 2F).

Antennes plus courtes que la tête. Les articles antennaires I, II, III, IV ont une taille relative de l'ordre de 18, 24, 43, 21 µm. Les cinq sensilles cylindriques (a-e) de l'article IV sont bien visibles avec b et e plus développées ; les microsensilles f et g sont présentes. La vésicule apicale globuleuse et granuleuse se détache du tégument par son pédoncule. L'organe antennaire III comprend deux microsensilles tubulaires logées derrière un repli tégumentaire, encadrées par trois sensilles épaisses dont deux courbées l'une vers l'autre, sur la face ventrale une sensille épaisse en position transversale (Fig. 2B-C).

La chétotaxie dorsale de la tête et du corps (Fig. 2A) met en évidence la répartition des différentes soies. Sur la tête sont macrochètes les soies a0 (19 µm), g3 (22 µm) et p5 (25 µm), sont mésochètes sd4 (16 µm), oc2 (16 µm), c5, p1 et p3. Organe postantennaire à six vésicules allongées caractéristiques du genre (Fig. 2E), les grains tégumentaires bordant la gouttière mesurent 2,5 µm. La répartition des soies est symétrique, certaines d'entre elles sont épaissies : p5 d'abdo-

men II, p3 d'abdomen III, p4 d'abdomen IV, p5 d'abdomen V, a1 d'abdomen VI et la soie antérieure latérale d'abdomen II et III. Sur la face ventrale l'aire génitale porte 1 + 1 soies épaissies (Fig. 2D) ; les sternites thoraciques de I à III portent 0, 1, 1 paires de soies.

La répartition des pseudocelles par demi-tergite correspond à la formule suivante 11/122/22221 ; de forme circulaire (8-9 µm) ils présentent un bord en forme de croissant avec généralement trois crêtes internes.

Pattes sans soies différenciées, griffes sans dent ni empodium. Tube ventral avec 7 + 7 soies (Fig. 2D).

Discussion

La répartition et le nombre des soies dorsales sur le thorax et sur l'abdomen sont remarquablement constants parmi les espèces décrites du genre à l'exception de *F. deharvengi* Rusek, 1991 où m4 fait défaut sur l'abdomen IV. Sur l'exemplaire, l'absence des soies m3 (abdomen I et II) et p4 (abdomen I et III) ne peut être considérée comme définitive. Lucianez & Simon (1992) ont utilisé les soies céphaliques comme critère discriminatoire accessoire des espèces (Tableau 1). De toutes les espèces, *F. cubanica* Rusek, 1991 est celle qui possède le plus grand nombre de microchètes céphaliques ; cet exemplaire est plus proche de *F. duplex* (Gama, 1962).

Si l'analyse détaillée de la chétotaxie rend la détermination difficile, les *Fissuraphorura* ont toutes un tégument à granulation fine. *F. deharvengi* présente un tégument plus grossier sur l'abdomen VI et deux épines, caractères interprétés par l'auteur comme une possible écomorphose. Ce spécimen se distingue aisément par son tégument grossier sur l'ensemble de la face dorsale et la soie a1 du tergite VI seulement épaissie à la base. Le tissu adipeux est normal ; le tube digestif est visible, rempli de nourriture, faits qui ne plaident pas en faveur d'une forme écomorphique.

CONCLUSIONS

Le climat sec et chaud qui règne sur ces deux massifs conditionne les populations de la faune du sol dépendantes des précipitations. Les prélèvements de mai et d'octobre ne sont pas très favorables, les formes juvéniles sont nombreuses et les adultes limités à quelques exemplaires. Compte tenu des variations individuelles chez les Onychiuridae, l'identification de certaines espèces s'avère difficile. Cette note complète nos connaissances sur les collemboles de Yougoslavie et les genres *Doutnacia* et *Fissuraphorura* sont cités pour la première fois dans cette région.

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Review of Giraud's types of the species of *Synergus* Hartig, 1840 (Hymenoptera, Cynipidae)

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KEY WORDS
Hymenoptera, Cynipidae, synergini, *Synergus*, Giraud, lectotypes, systematics, synonymies, hosts.

ABSTRACT
In this work the typical series of the remaining *Synergus* species described by Giraud are studied. The lectotypes of each one are designated. *Synergus consobrinus* is redescribed, *S. variabilis* Mayr, 1872 (= *S. cerridis* n.syn.) (= *S. conformis* n.syn.) and *S. diaphanus* are characterized. The respective synonymies for the rest of the studied species are established. Finally, biological data of some of the species are given and the distribution area of some of them is widened.

MOTS CLÉS
Hymenoptera, Cynipidae, synergini, *Synergus*, Giraud, lectotypes, systématique, synonymies, hôtes.

RÉSUMÉ
Révision des espèces-types du genre Synergus *Hartig, 1840 (Hymenoptera, Cynipidae).* Dans ce travail, nous étudions le matériel des séries de types décrites par Giraud concernant le genre *Synergus*. Les lectotypes de ces séries sont désignés. Nous redécrivons l'espèce *Synergus consobrinus* ; les espèces *S. variabilis* Mayr, 1872 (= *S. cerridis* n.syn.) (= *S. conformis* n.syn.) et *S. diaphanus* sont caractérisées. Nous établissons les synonymies concernant les autres espèces du genre. Pour chaque espèce nous mentionnons les principales caractéristiques biologiques et la répartition.

INTRODUCTION

Joseph-Étienne Giraud (1808-1877) was one of the greatest cynipidologists of the last century. His Cynipidae studies, though few in number (Giraud 1859, 1866, 1868a, b, 1871; Darboux & Houard 1907; Laboulbène 1877), greatly lead to the recognition of a large number of cynipid gall-forming species. He described more than forty species as well as the new genus *Dryocosmus*. A part of the author's research was compiled in an unpublished manuscript deposited in the Muséum national d'Histoire naturelle, Paris (MNHN). Houard (1911) published a version of Giraud's manuscript. In this publication eleven new *Synergus* species are described: *S. apertus*, *S. cerridis*, *S. clavatus*, *S. conformis*, *S. consobrinus*, *S. diaphanus*, *S. hartigi*, *S. inflatus*, *S. longiventris*, *S. subterraneus* and *S. vesiculosus*. The study also contains descriptions of four new cynipids not belonging to the *Synergus* species.
The only species of *Synergus* that has previously been examined is *S. apertus*, which was synonimyzed with *Saphonecrus undulatus* (Mayr 1872) by Pujade-Villar & Nieves-Aldrey (1990).
Giraud's material was drawn largely from Central Europe. In his manuscript there is no mention either of the origin of specimens.
The study of the *Synergus* species type material is especially interesting in the Palaearctic zone, since some doubt has been cast on thirty-one of the fifty-nine species described.

ABBREVIATIONS

NMW	Naturhistorisches Museum, Wien
MNCNM	Museo Nacional de Ciencias Naturales, Madrid
MNHN	Muséum national d'Histoire naturelle, Paris
ZSBS	Zoologische Staatssammlung, München

SEM METHODS

The SEM photographs of the type material *Synergus consobrinus* were taken without any coating. The voltage used ranged between 200 and 1000 V, depending on the specimens. In this way we were able to obtain pictures while preserving the specimen types without any manipulation. The pictures of *S. variabilis* were obtained by gold coating of one of the dissected *S. cerridis* specimens.

LIST OF SPECIES

Giraud's nominal species described in *Synergus* genus by Houard (1911) are dealt with below. The heading for each species treatment is the currently accepted name. For each species the lectotypes are designated. The synonymous names, hosts, distribution and information concerning type material are given. The main taxonomic aspects are discussed. Giraud's accepted species and *S. variabilis* Mayr are characterized and differentiated from the closely related species using a taxonomical key.

Saphonecrus haimi (Mayr, 1872)

Sapholitus haimi Mayr, 1872. *Verh. Ges. Wien* 22: 723. Types in NMW.

Synergus clavatus Giraud (*in* Houard 1911: 333), n.syn.

Saphonecrus haimi (Mayr), *in* Pujade-Villar *et* Nieves-Aldrey, 1990: 53 (misspelling), n.syn.

TYPE MATERIAL. — Lectotype ♀, and paralectotypes: 1 ♂ and 4 ♀♀ of *Saphonecrus haimi* have been designated *in* Pujade-Villar & Nieves-Aldrey (1990). Lectotype ♀ of *Synergus clavatus* Giraud, here designated, mounted on micro-pin; paralectotypes, 32 ♂♂ and 5 ♀♀, all of them mounted on micro-pins.

DISTRIBUTION. — Central Europe and Israel in Cynipid galls of *Quercus cerris* and *Q. ithaburensis*.

HOSTS. — Hymenoptera, Cynipidae, Cynipini: *Chilaspis nitidus* (Giraud, 1859) ♂, *Neuroterus lanuginosus* (Giraud, 1859) ♂, *N. saliens* (Kollar, 1857) ♂ and *N. minutus* (Giraud, 1859) ♂. Diptera., Cecidomyiidae: *Janetia cerris* (Kollar, 1850).

COMMENTS
This species and *Saphonecrus undulatus* (Mayr, 1872) are close to *Synergus* genus because they have pronotal carina as do most of the species of *Synergus* Pujade-Villar & Nieves-Aldrey (1990). The *Neuroterus minutus* galls is a new host record of *Saphonecrus haimi*.

Synergus variabilis Mayr, 1872
(Figs 1-3)

Synergus variabilis Mayr, 1872. *Verh. Ges. Wien* 22: 702. Types in NMW.
Synergus cerridis Giraud (*in* Houard, 1911: 331-332), n.syn.

Synergus conformis Giraud (*in* Houard, 1911: 333-334), n.syn.

Synergus cerricolus Vasileva-Samnalieva, 1986, n.syn.

TYPE MATERIAL. — The paralectotypes of *Synergus variabilis* Mayr (1 ♂ and 2 ♀♀), mounted on micropins, have been examined. Lectotype ♂ of *Synergus cerridis* Giraud, here designated, mounted on micropin; paralectotypes: 15 ♂♂ and 26 ♀♀, all of them mounted on micro-pins. Lectotype ♂ of *Synergus conformis* Giraud, here designated, mounted on micro-pin; paralectotypes: 17 ♂♂ and 16 ♀♀, mounted on micro-pins; 1 ♀, on card.

DISTRIBUTION. — Central Europe and Israel in Cynipid galls of *Quercus cerris* and *Q. ithaburensis*.

HOSTS. — Hymenoptera, Cynipidae, Cynipini: *Andricus grossulariae* Giraud, 1859 ♂♀, *Aphelonyx cerricola* (Giraud,1859) ♂, *Chilaspis nitidus* (Giraud, 1859) ♂, *Dryocosmus cerriphilus* Giraud, 1859 ♂, *Neuroterus lanuginosus* (Giraud, 1859) ♂ and *N. macropterus* (Hartig, 1843) ♂; Synergini: *Synophrus politus* Hartig, 1843. Diptera, Cecidomyiidae: *Dryomyia circinnans* (Giraud, 1861) and *Janetia cerris* (Kollar, 1850).

COMMENTS
This species is a cynipid galls inquiline in *Q. cerris* belonging to Section II of *Synergus*. Kieffer (1902) differentiated four chromatic variations. Quinlan (1978) redescribed this species but he made a number of errors. Firstly, the tarsal claws are not simple, rather they have a small tooth, not pointed and usually hidden by the arolium; secondly, and more importantly: all type material examined does not have a pronotal carina (Fig. 1A) although when viewed dorsally the pronotum is angular at the lateral corners (Fig. 1B). Only the species *Synergus plagiotrochi* does not have a lateral pronotal carinae. This species is typical in the Mediterranean region on cynipid-galls of *Plagiotrochus*. This species is closely related to *S. apicalis* and *S. rotundiventris*.

In order to distinguish these morphologically closely related species a dichotomic key is provided:

1. Lateral pronotal carina present. Punctures on upper face usually distinct. Inquilines frequently associated with shoots *Quercus*, usually deciduous *Quercus* ..... *

— Lateral pronotal carina absent. Punctures on upper face usually obsolete 2

2. Radial cell open on margin. In dorsal view lateral pronotum is rotund. Punctuation on upper face and frontal carina always obsolete. Inquiline in galls of species of *Plagiotrochus* genus on evergreen oaks *Q. ilex* and *Q. coccifera* .... *S. plagiotrochi* Nieves-Aldrey *et* Pujade-Villar, 1986

— Radial cell closed. In dorsal vision the pronotum is angular in the lateral corners. Punctuation on upper face and frontal carina present in larger specimens. Inquiline in several galls of *Neuroterus* associated to *Q. cerris*, mainly *N. macropterus* and *N. lanuginosus* ..... *S. variabilis* Mayr, 1872

* A complex of two closely related species: *S. apicalis* Hartig, 1841 and *S. rotundiventris* Mayr, 1872, that cannot be satisfactorily distinguished by external morphological characteristics. The intraspecific variation is great and the limits are not clear.

Other notable features include: vertex not punctuated in small specimens (Fig. 2A) and with weak punctuation in large specimens (Fig. 2B); lateral frontal carinae present but not very clear (Fig. 2); second antennomere very long in large specimens, always longer than they are broad and larger than third antennomere; male with first flagellomere weakly expanded basally and apically (Fig. 3); mesonotum with interrupted, sharp and widely-spaced transverse rugae

(Fig. 1); notauli shallow and short, faint or absent at least in anterior one third of mesoscutum; notauli shallow and short, faint or absent at least in the anterior third of mesoscutum, and medial impression very short or absent (Fig. 1B); mesopleuron usually ventrally smooth and shiny (Fig. 1A); radial cell closed on margin.

The material of Giraud belonging to *S. cerridis* and *S. conformis* is the same as that belonging to *S. variabilis*. This series has all of the chromatic variations described by Kieffer (1902). Even though the type series of *Synergus cerricolus* Vassileva-Samnalieva were not examined, after the examination of the type material of *S. variabilis* Mayr, 1872 and Giraud's type series as well as the original description of the former species, we conclude that *Synergus cerricolus* is a junior synonym of *S. variabilis*.

The mention of *Neuroterus saliens* and *Janetia cerris* as a *Synergus variabilis* host is interesting because they are new for *S. variabilis*. Finally, the specimens of *S. variabilis* collected in *Janetia cerris*, deposited in Giraud's collection, are important as this species was mentioned in Cecidomyiidae galls (*Dryomyia circinnans* Giraud, 1861, by Mayr, 1872) and it has been considered dubious as it has not been confirmed by subsequent authors.

Synergus thaumacerus (Dalman, 1823)

Cynips thaumacera Dalman, 1823. *Analecta Ent.*: 96. Location of types unknown.

Synergus luteus Hartig, 1840. *Z. Ent. Germar* 2: 199. – Mayr 1872.

Synergus klugii Hartig, 1840. *Z. Ent. Germar* 2: 199. – Mayr 1872.

Synergus carinatus Hartig, 1841. *Ent. Germar* 3: 348. – Mayr 1872.

Synergus thaumatocerus Dalla Torre, 1893. *Cat. Hym.* 2: 114 (unjustified emendation).

Synergus vesiculosus Giraud (*in* Houard 1911: 323-234), n.syn.

Synergus inflatus Giraud (*in* Houard 1911: 324-325), n.syn.

TYPE MATERIAL. — Giraud's collection. Lectotype ♂ of *Synergus vesiculosus* Giraud, here designated, mounted on micro-pin; paralectotypes: 5 ♂♂ and 10 ♀♀, all of them mounted on micro-pins. Lectotype ♂ of *Synergus inflatus* Giraud, here designated, mounted on micro-pin; paralectotypes: 22 ♂♂ and 27 ♀♀, all of them mounted on micro-pins.

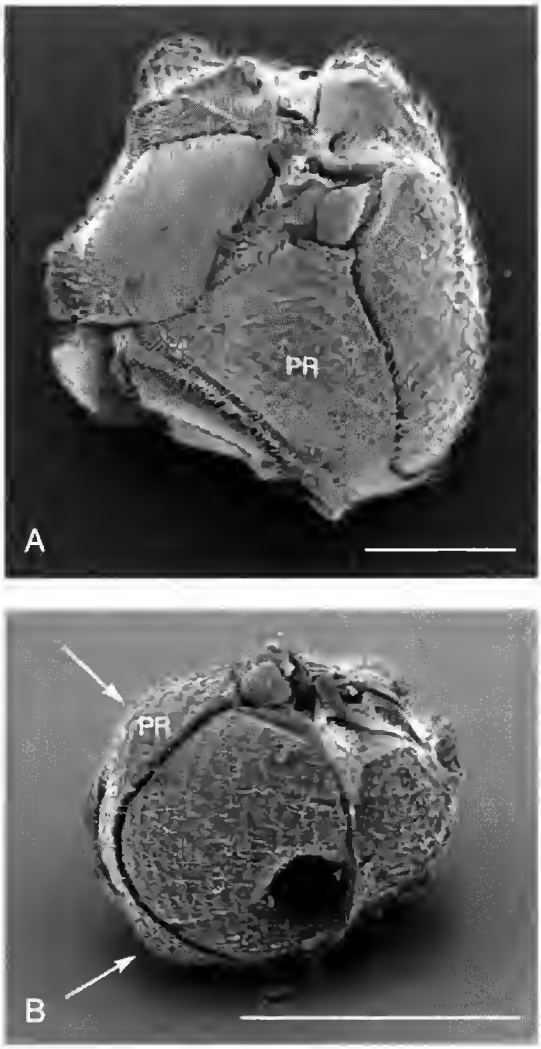

FIG. 1. — Thorax of *S. variabilis* Mayr; **A**, lateral view. **B**, dorsal view. PR, pronotum. See text for additional discussion. Scale bars: a, 200 µm; B, 500 µm.

DISTRIBUTION. — Western Palaearctic in Cynipid galls of *Quercus cerris*, *Q. faginea*, *Q. humilis*, *Q. petraea*, *Q. pyrenaica* and *Q. robur*.

HOSTS. — Only Cynipini: *Andricus anthracinus* (Curtis, 1838) ♂, *A. curvator* Hartig, 1840 ♂♀, *A. cydoniae* Giraud, 1859 ♂♀, *A. singulus* Mayr, 1870

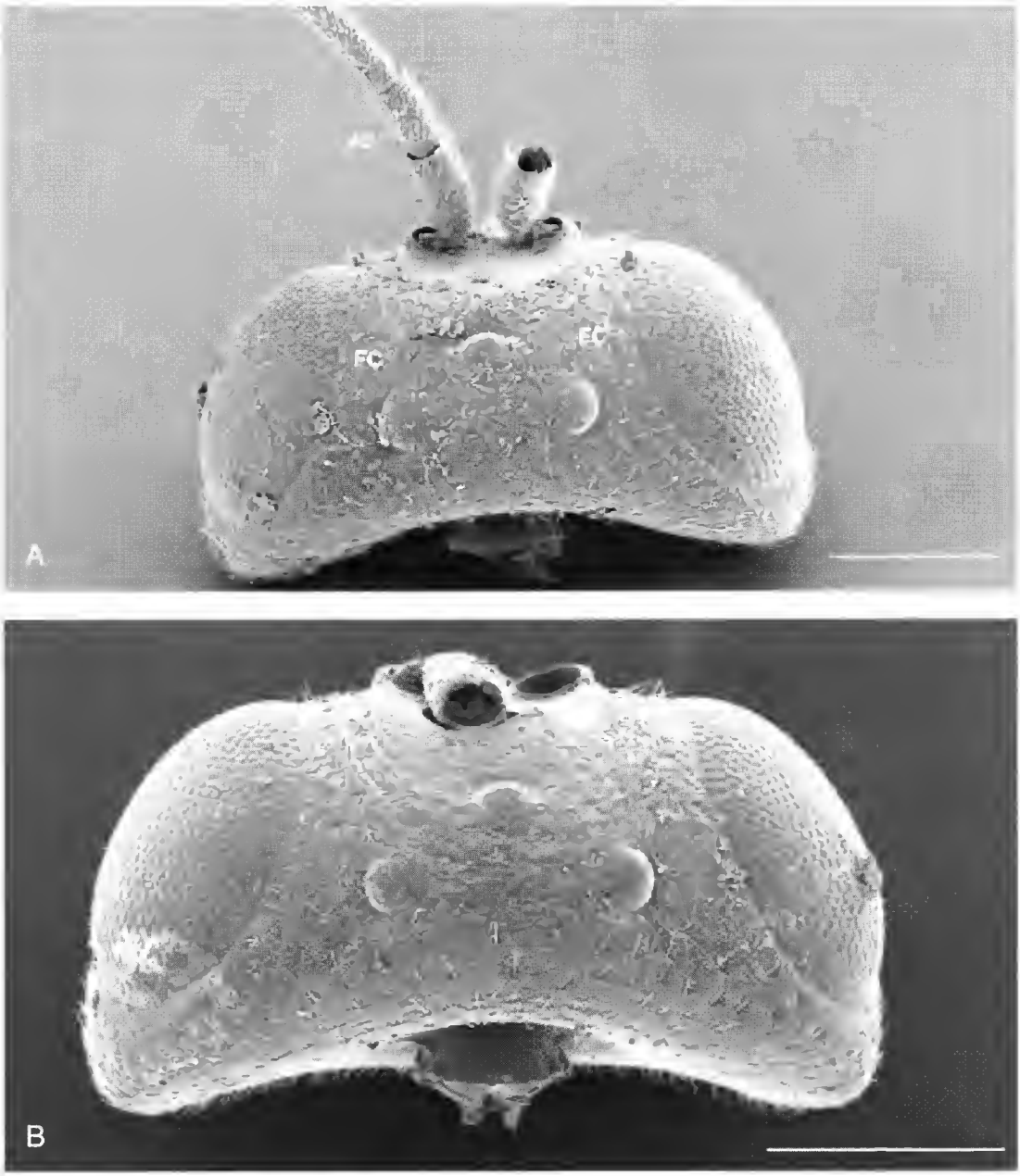

FIG. 2. — Head of *S. variabilis* Mayr, dorsal view; **A**, small specimen; **B**, large specimen. A, antennomere; FC, faciel carinae. See text for additional discussion. Scale bars: 200 µm.

ŏ, *A. gallaeurnaeformis* (Boyer de Fonscolombe,1832) (= *suflator* Mayr, 1882) ♂ ♀, *A. gallaetinctoriae* (Olivier, 1791) ŏ, *Aphelonyx cerricola* (Giraud,1859) ŏ, *Cynips disticha* Hartig, 1840 ŏ, *C. quercusfolii* L., 1758 ŏ, *Dryocosmus cerriphilus* Giraud, 1859 ŏ, *D. nervosus* (Giraud,1859) ♂ ♀, *Neuroterus saliens* (Kollar, 1857), ♂ ♀, *N. saliens* (= *glandiformis* Kaltenbach, 1867) ŏ, *N. quercusbaccarum* (L., 1758) ♂ ♀, *N. quercusbaccarum* (= *lenticularis* Olivier, 1791) ŏ, *N. tricolor* (Hartig, 1841) ♂ ♀, *N. tricolor* (= *fumi-*

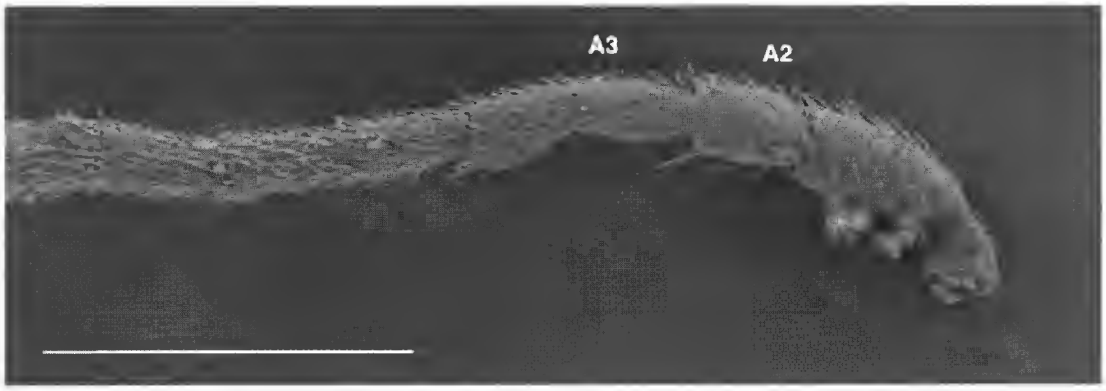

FIG. 3. — First male antennomeres of *S. variabilis* Mayr. Scale bar: 200 µm.

pennis Hartig, 1841) ♂, *Trygonaspis megaptera* (Panzer, 1801) ♂ ♀, *T. megaptera* (= *renum* Hartig, 1840) ♂, *T. mendesi* Tavares, 1901 ♂ and *T. synaspis* (Hartig, 1841) ♂ ♀, *Synophrus politus* Hartig, 1843.

COMMENTS

The characters for recognizing *S. thaumacerus* are described in Nieves-Aldrey & Pujade-Villar (1986). Giraud's material of *S. vesiculosus* and *S. inflatus* do not differ from that of *S. thaumacerus*. The hosts *Andricus gallaetinctoriae* and *Dryocosmus cerriphilus* and *Synophrus politus* are new to *S. thaumacerus*.

Synergus subterraneus Giraud (*in* Houard, 1911: 335)

Synergus latifrons Nieves-Aldrey *et* Martin-Chicote, 1985. *Bol. Asoc. esp. Entom.* 9: 151. n.syn. Types in MNCNM.

TYPE MATERIAL. — Of Giraud's collection. Lectotype ♀, here designated, mounted on micro-pin; paralectotypes: 8 ♀♀ mounted on micro-pins; 3 ♀♀ on carts.

DISTRIBUTION AND HOSTS. — Only Cynipini: Spain in *Andricus sieboldi* (Hartig, 1843) ♂ on *Quercus pyrenaica* and in central Europe (country unknown) in *Andricus rhyzomae* (plant-host unknow, probably *Q. humilis* (= *pubescens*) because Giraud (*in* Houard, 1911) collected *A. rhyzomae* in *Q. humilis*).

COMMENTS

The width of the head in frontal vision is a very specific character of this species, since the transfacial line is at least twice as long as the height of the compound eye. The biology is associated with subterraneous galls of *Andricus*.

Synergus albipes Hartig, 1841

Synergus albipes Hartig, 1841. *Z. Ent. Germar* 3: 349. Types in ZSM.

Synergus erythrocerus Hartig, 1841. *Z. Ent. Germar* 3: 349. – Mayr 1872.

Synergus varius Hartig, 1841. *Z. Ent. Germar* 3: 349. – Eady 1952.

Synergus tristis Mayr, 1873. *Verh. Ges. Wien* 22: 715. – Eady 1952.

Synergus nervosus Hartig, *sensu* Ross, 1951. *Trans Soc. Brit. Entom.* 2 (3): 92. – Eady 1952.

Synergus nervosus f. *albipes* Ross, 1951. *Trans Soc. Brit. Entom.* 2 (3): 91. – Eady 1952.

Synergus nervosus f. *tristis* Ross, 1951. *Trans Soc. Brit. Entom.* 2 (3): 93. – Eady 1952.

Synergus mutabilis Dettmer, 1924. *Natuurhist. Maandbl.* 13: 147. – Wiebes-Rijks 1979.

Synergus hartigi Giraud (*in* Houard 1911: 332) n.syn.

TYPE MATERIAL. — Of Giraud's collection. Lectotype ♂, here designated, mounted on micro-pin; paralectotypes: 10 ♂♂ and 11 ♀♀, all of them mounted on micro-pins.

DISTRIBUTION. — West Palaearctic in Cynipid galls of *Quercus cerris*, *Q. canariensis*, *Q. faginea*, *Q. humilis*, *Q. petraea*, *Q. pyrenaica*, *Q. suber* and *Q. robur*.

HOSTS. — Only Cynipini: *Andricus anthracinus* (Curtis, 1838) ♂, *A. amblycerus* (Giraud, 1859) ♂, *A. caliciformis* (Giraud, 1859) ♂, *A. callidoma* Hartig, 1841 ♂, *A. capudmedusae* (Hartig, 1843) ♂, *A. clementinae* (Giraud, 1859) ♂, *A. conglomeratus* (Giraud, 1859) ♂, *A. coriarius* Hartig, 1843 ♂, *A. corruptrix* (Schlechtendal, 1870) ♂ *A. curvator* Hartig, 1840 ♂♀, *A. fecundator* (Hartig, 1840) ♂, *A. gallaetinctoriae* (Olivier, 1791) ♂, *A. gallaeurnaeformis* (Boyer de Fonscolombe,1832) ♂, *A. glutinosus* (Giraud, 1859) ♂, *A. hartigi* (Hartig, 1843) ♂, *A. hungaricus* (Hartig, 1843) ♂, *A. globuli* (Hartig, 1840) ♂, *A. kollari* (Hartig, 1843) ♂, *A. lignicolus* (Hartig, 1840) ♀, *A. lucidus* (Hartig, 1843) ♂, *A. nudus* (Adler,1881) ♂ (= *malpighii* Adler, 1881), *A. polycerus* (Giraud, 1859) ♂, *A. quadrilineatus* Hartig, 1840 ♂, *A. quercuscalicis* (Burgsdorf, 1679) ♂, *A. quercusramuli* (L., 1761) (= *autumnalis* Hartig, 1840) ♂, *A. quercustozae* (Bosc, 1792) ♂, *A. seminationis* (Giraud, 1859) ♂, *A. solitarius* (Boyer de Fonscolombe, 1832) ♂, *Cynips agama* Hartig, 1840 ♂, *C. disticha* Hartig, 1840 ♂, *C. longiventris* Hartig, 1840 ♂, *C. quercus* (Fourcroy, 1785) ♂, *C. quercusfolii* L., 1758 ♂, *Neuroterus albipes* (Schenck, 1863) ♂ (= *laevisculus* Schenck, 1863), *N. lanuginosus* Giraud, 1859 ♂, *N. numismalis* (Fourcroy, 1785) ♂, *N. numismalis* (= *vesicator* Schlechtendal, 1870) ♂♀, *N. saliens* (Kollar, 1857) ♂, *N. quercusbaccarum* (L., 1758) ♂♀, *N. quercusbaccarum* (= *lenticularis* Olivier, 1791) ♂, *N. tricolor* (Hartig, 1841) ♂♀, *N. tricolor* (= *fumipennis* Hartig, 1841) ♂, *Plagiotrochus amenti* Tavares, 1902 ♂♀, *Trygonaspis bruneicornis* Tavares, 1902 ♂, *T. megaptera* (Panzer, 1801) (= *renum* Hartig, 1840) ♂, *T. mendesi* Tavares, 1901 ♂ and *T. synaspis* (Hartig, 1841) ♂♀.

COMMENTS

This species has a large number of hosts, most of which are agamic in form. Nevertheless, it seems not to be a specific feature. This species is very closely related to *S. nervosus* Hartig, 1840, and sometimes there are no clear differences between them. The first flagellomere segment (of all the males of *S. hartigi* have) is moderately expanded apically and, usually the second antennomere in both sexes are as long as they are broad or slightly longer. For these reasons, we believe that *S. hartigi* is synonymous of *S. albipes*. *Andricus hartigi* is a new host of this species.

Synergus gallaepomiformis
(Boyer de Fonscolombe, 1832)

Diplolepis gallae-pomiformis Boyer de Fonscolombe, 1832. *Ann. Sc. Nat.* 26: 195. Location of types unknown.

Synergus facialis. Hartig, 1840. *Z. Ent. Germar* 2: 199. – Dalla Torre & Kieffer 1910.

Synergus vulgaris Hartig, 1840. *Z. Ent. Germar* 2: 198. – Ross 1951.

Synergus bispinus. Hartig, 1841. *Z. Ent. Germar* 3: 347. – Mayr 1872.

Synergus erythrocerus var. 1 *et* 2 Hartig, 1844. *Z. Ent. Germar* 3: 349.

Aulax albinervis Snellen van Vollenhoven, 1869: *Tijdschr. Ent.* 12: 126. – Kieffer 1902.

Synergus pomiformis Kieffer, 1898. *Wien Ent. Zeit.* 17: 264 (not Ashmead, 1885), unjustified emendation.

Synergus gallaepomiformis gallaepomiformis Dalla Torre *et* Kieffer, 1910. *Das Tierreich* 24: 621.

Synergus gallaepomiformis gallicus Dalla Torre *et* Kieffer, 1910. *Das Tierreich* 24: 622.

Synergus gallaepomiformis var. *minima* Kieffer, 1899. *André, Spec. Hym. Europ.* 7 (I): 358.

Synergus gallaepomiformis minimus Kieffer, Dalla Torre *et* Kieffer, 1910. *Das Tierreich* 24: 622.

Synergus maculatus Tavares, 1920. *Mem. Port. Sc. Nat. Zool.* 4: 47-49. – Nieves-Aldrey *et* Pujade-Villar, 1986.

Synergus longiventris Giraud (*in* Houard, 1911: 318-319). n.syn.

TYPE MATERIAL. — Giraud's collection. Lectotype ♀, here designated, mounted on micro-pin; paralectotypes: 9 ♂♂ and 17 ♀♀, all of them mounted on micro-pins.

DISTRIBUTION. — West Palaearctic *in* Cynipid galls of *Quercus cerris*, *Q. faginea*, *Q. humilis*, *Q. petraea*, *Q. pyrenaica*, and *Q. robur*.

HOSTS. — Only Cynipini: *Andricus anthracinus* (Curtis, 1838) ♂, *A. callidoma* Hartig, 1841 ♂, *A. capudmedusae* (Hartig, 1843) ♂, *A. clementinae* (Giraud, 1859) ♂, *A. conglomeratus* (Giraud, 1859) ♂, *A. coriarius* Hartig, 1843 ♂, *A. coronatus* (Giraud *in* Houard 1911) ♂, *A. corruptrix* (Schlechtendal, 1870) ♂, *A. curvator* Hartig, 1840 ♂♀, *A. curvator* (= *collaris* Hartig, 1840) ♂, *A. fecundator* (Hartig, 1840) ♂, *A. gallaetinctoriae* (Olivier, 1791) ♂, *A. gallaeurnaeformis* (Boyer de Fonscolombe, 1832) ♂, *A. glandulae* (Hartig, 1840) ♂, *A. glutinosus* (Giraud, 1859) ♂, *A. hartigi* (Hartig, 1843) ♂, *A. hungaricus* (Hartig, 1843), ♂, *A globuli* (Hartig, 1840) ♂, *A. kollari* (Hartig, 1843) ♂, *A. legitimus* Wiebes-Rijks, 1980 ♂, *A. lignicolus* (Hartig, 1840) ♀, *A. nudus* (Adler,1881) ♂ (= *malpighii* Adler, 1881), *A. paradoxus* (Rad, 1866), *A. quadrilineatus* Hartig, 1840 ♂, *A. quercuscalicis* (Burgsdorf, 1679) ♂, *A. quercuscorticis* (L., 1761) ♂,

A. quercusradicis (Fabricius, 1798) ♂, *A. quercusradicis* (= *trilineatus* Hartig, 1840) ♂ ♀, *A. quercusramuli* (Linnaeus, 1761) ♂ ♀, *A. quercusramuli* (= *autumnalis* Hartig, 1840) ♂, *A. quercustozae* (Bosc, 1792) ♂, *A. seminationis* (Giraud, 1859) ♂, *A. solitarius* (Boyer de Fonscolombe, 1832) ♂, *A. sieboldi* (Hartig,) ♂, *Callirhytis glandium* (Giraud, 1859) ♂, *Cynips disticha* Hartig, 1840 ♂, *C. divisa* Hartig, 1840 ♂, *C. longiventris* Hartig, 1840 ♂, *C. longiventris* Hartig, 1840 (= *similis* Adler, 1881) ♂ ♀, *C. quercusfolii* Linnaeus, 1758 ♂, *C. quercusfolii* (= *taschenbergi* Selechtendal, 1870) ♂ ♀, *Neuroterus albipes* (Schenck, 1863) ♂ (= *laevisculus* Schenck, 1863), *N. lanuginosus* Giraud, 1859 ♂, *N. numismalis* (Fourcroy, 1785) ♂ *N. quercusbaccarum* (Linnaeus, 1758) ♂ ♀, *N. quercusbaccarum* (= *lenticularis* Oliviet, 1791) ♂, *N. tricolor* (Hartig, 1841) ♂ ♀, *N. tricolor* (= *fumipennis* Hartig, 1841) ♂, *Trygonaspis megaptera* (Panzer, 1801), *T. megaptera* (= *renum* Hartig, 1840) ♂, and *T. synaspis* (Hartig, 1841) ♂ ♀.

COMMENTS

This species has a very large number of hosts, most of them belong to the agamic form. Nevertheless, it seems not to be a specificity in some gall models. Moreover, this species shows a major morphological variability. Giraud described *S. longiventris* according to gastral length. Certainly, Giraud was right, but the males and females (without gaster) are the same as the largest specimens of *S. gallaepomiformis*. For this reason, we believe that gaster length is a new variable caracter of this species. Furthermore, all the hosts of *S. longiventris* mentioned by Giraud have been cited in *S. gallaepomiformis*.

Synergus diaphanus Giraud (*in* Houard, 1911: 317-318)

TYPE MATERIAL. — Giraud's collection. Lectotype ♂, here designated, mounted on micro-pin; paralectotypes: 2 ♂♂ and 7 ♀♀, all of them mounted on micro-pins.

DISTRIBUTION AND HOSTS. — Only Cynipini: in Central Europe (country unknown) in *Andricus gallaetinctoriae* (Olivier, 1791) ♂ [*Quercus caducifolius* host unknown; Giraud (*in* Houard 1911) mentioned that *A. gallaetinctoriae* was collected in *Q. petraea*, *Q. robur* and *Q. humilis*].

COMMENTS

Section I species with the medial mesoscutal impression are easy to differentiate. *Synergus diaphanus* is closely related to *S. ibericus* because it has the same morphology and similar ecology; *S. ibericus* is a species inquiline of *A. kollari* ♂ and *S. diaphanus* to *A. gallaetinctoriae*; both host species make spherical galls (10-20 mm) with superficial protuberances (sometimes absent in *A. kollari*) but the galls of *A. gallaetinctoriae* are harder. Probably they are sister species. In order to distinguish these species the following characters may be used:

1. Radial cell 3.0 times longer than wide; R2 vein straight line. Antenna light, orange; last flagellomere segments almost 2 × 1. Inquiline in galls of *Andricus kollari* (in Iberian Peninsula) ..... *S. ibericus* Tavares, 1920

— Radial cell shorter, 2.5 to 2.7 times longer than wide; R2 vein curved. Antenna colour dark, brown; last flagellomere segments shorter, almost 1.5 times longer than wide. Inquiline in galls of *Andricus gallaetinctoriae* (not present in Iberian Peninsula) ..... *S. diaphanus* Giraud (*in* Houard 1911)

Synergus consobrinus Giraud (*in* Houard 1911)

TYPE MATERIAL. — Giraud's collection. Lectotype ♂, here designated, mounted on micro-pin; paralectotypes: 1 ♂ and 9 ♀♀, all of them mounted on micro-pins.

DISTRIBUTION AND HOSTS. — Only Cynipini: in Central Europe (country unknown) in *Andricus grossulariae* Giraud, 1859 probably in *Q. cerris* according to Giraud, 1859.

REDESCRIPTION

Male

Length 1.5-2.1 mm. Head with a yellow coloration more or less expanded; vertex black and

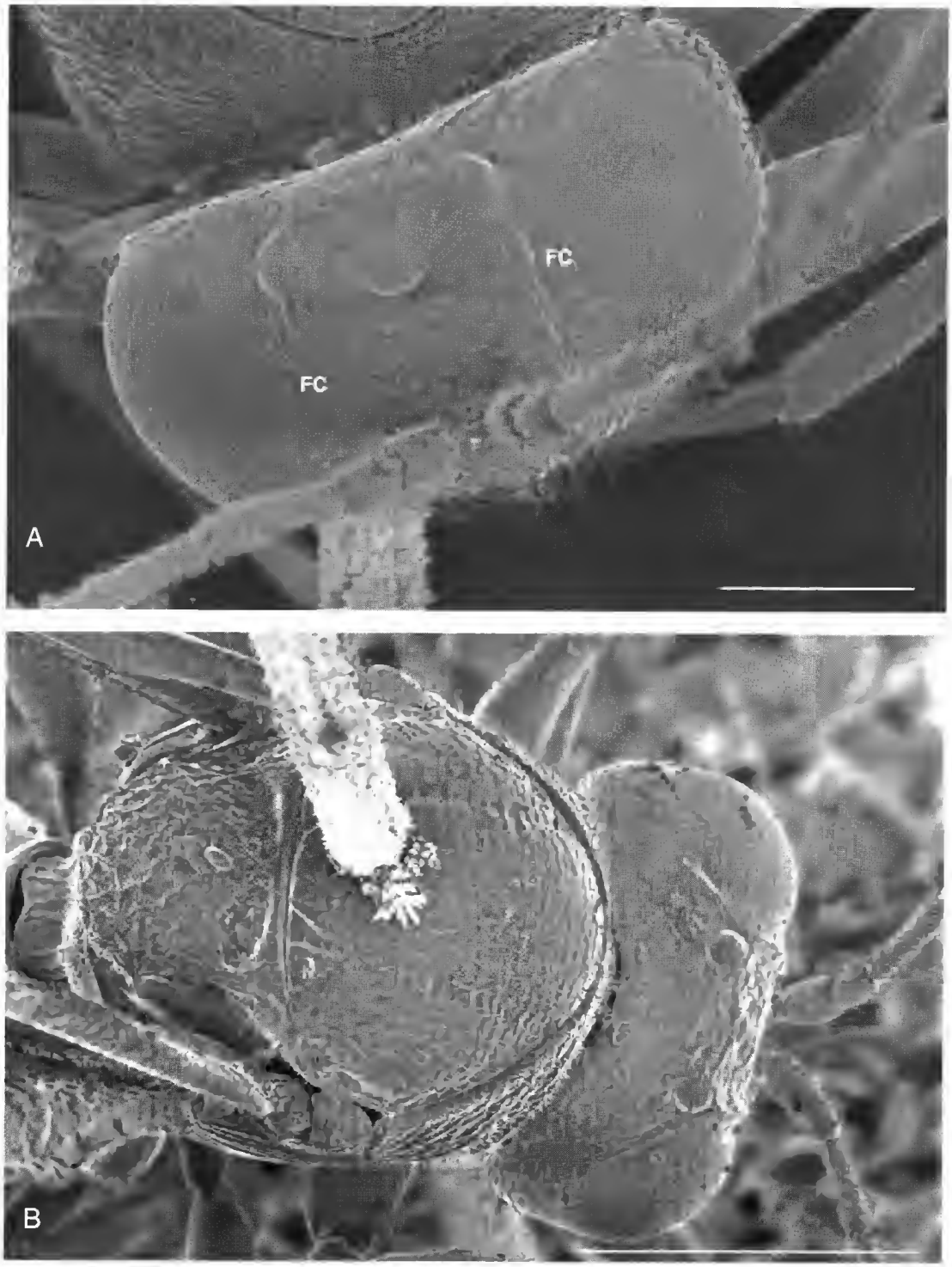

FIG. 4. — *Synergus consobrinus* Giraud, dorsal view. **A**, head; **B**, thorax. FC, facial carinae. Scale bars: A, 200 µm; B, 500 µm.

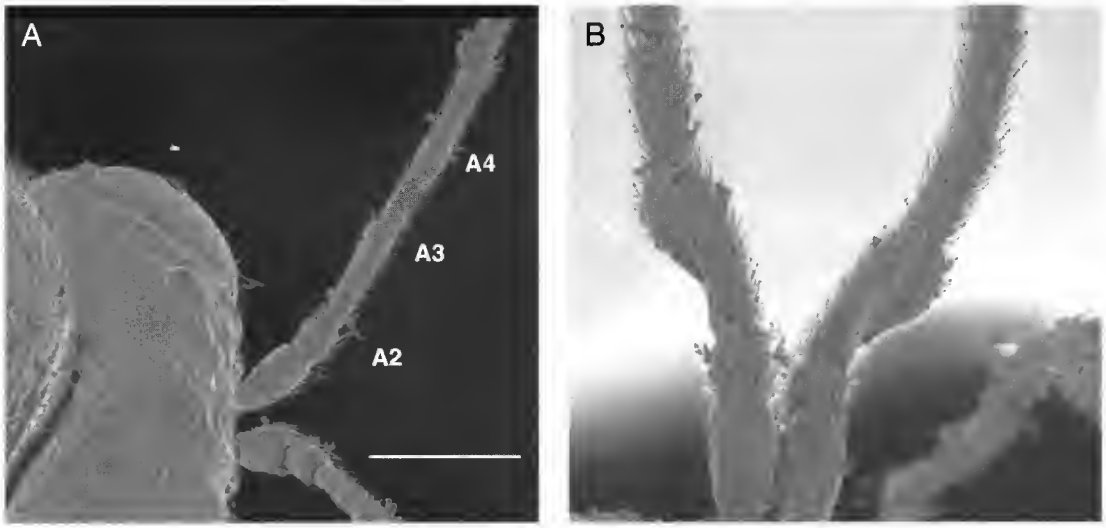

FIG. 5. — **A**, head and first female antennomeres of *S. consobrinus* Giraud; **B**, first male antennomeres of *S. consobrinus* Giraud. A, antennomeres. Scale bar: 200 µm.

cheeks from yellow to red; thorax black; gaster red; legs light between yellow and brown; wing venation light brown. Head, in dorsal view, about two times broader than long; in frontal view, triangular and slightly broader than long; face radiating striate with strias to the toruli; front coriarious without punctures in small specimens and with punctures in large specimens; lateral frontal carinae strong and not branched near ocelli (Fig. 4); vertex coriarious-rugose not punctuated or with scattered shallow punctures without subparallel carinae running transversely between posterior ocelli; the diameter of the lateral ocelli is 2 and POL: OOL: OCO relation is 6: 3: 3; antenna with fifteen antennomeres (4: 2: 7: 4: 4: 4: 4: 4: 3,5: 3: 3: 3: 3: 3: 3); A2 is longer than broad; A3 is strongly expanded apically (Fig. 5B); those from A7 to A15 are thicker. Pronotum with coriarious sculpture and some longitudinal striae laterally; lateral pronotal carinae present; mesoscutum with coriarious sculpture; notauli (Fig. 4B) percurrent, not very deep and posteriorly not very broad; medial mesoscutal impression short; scutelar foveae ovate and sculptured with blurred posterior margins; mesopleuron longitudinally striate; parallel propodeal carinae, pubescent area between them. Radial cell of forewing closed, length from 2.5 to 2.7 times breadth. Gaster without punctuation, one smaller than thorax; abdominal terga 3 + 4 without pictures posteriorly or limited to an apical dorsal patch. Tarsal claws with a tooth.

Female

Differs from male as follows: length 1.5-2.5 mm; antenna with fourteen segments (5: 3: 7: 6: 6: 6: 5: 5: 4: 4: 3: 3: 3: 5); A2 longer than broad (Fig. 5A); A3 not modified. Face black and yellowish around mouth.

After examining the typical series of this species, we concluded that it is related closely to the *S. pallicornis*, *S. albipes* and *S. nervosus* group. Moreover, *S. consobrinus* is a cynipid-host in galls of *Andricus grossulariae*. Not one species of this species group has this host. *Andricus grossulariae* forms galls in catkins on *Q. cerris* (in Europe except the Iberian Peninsula) or on *Q. suber*.

We summarize the morphological differences of this group of species in the following dichotomical key to identification:

1. Lateral frontal carinae strong and often much branched near ocelli; subparallel carinae running transversely between posterior ocelli, and obliquely from each posterior ocellus to margin of occiput. First flagellomere long in both sexes; in females at least 1.5 times longer than second; in males curved in the middle and weakly expanded distally. Face always black ..... *S. pallicornis* Hartig 1841

— Lateral frontal carinae weak (where strong the face is not black) and branched or not near ocelli; vertex coriarious, usually without subparallel carinae running transversely between posterior ocelli. First flagellomere relatively shorter; in females less than 1.5 times longer than second; in males slightly expanded apically or curved in the middle and not expanded (where it is weakly expanded distally the face is yellow or yellowish red) 2

2. Lateral frontal carinae strong and complete. Males with first flagellomere weakly expanded distally. Face in males yellowish color and red in females. Inquilines in galls of *Andricus grossulariae* in *Q. cerris* .... *S. consobrinus* Giraud (*in* Houard, 1911)

— Lateral frontal carinae weak. Males with the first flagellomere segment different and face black. Females with the face black. Inquilines in a large number of Cynipid galls in *Quercus caducifolious* .... *S. albipes* Hartig, 1841 and *S. nervosus* Hartig, 1840

TAXONOMICAL SUMMARY AFTER THE GIRAUD'S TYPES REVIEW OF *Synergus*

SYNERGINI

Saphonecrus Dalla Torre *et* Kieffer, 1910

S. haimi (Mayr, 1872)
- *S. clavatus* Giraud (*in* Houard 1911) n.syn.
- *S. haymi* (Mayr); Pujade-Villar *et* Nieves-Aldrey, 1990: (misspelling), **n.syn.**

S. undulatus (Mayr, 1872)
- *S. apertus* Giraud (*in* Houard 1911)
- *S. giraudi* Pujade-Villar, 1985

Synergus Hartig, 1840

S. albipes Hartig, 1841
- *S. hartigi* Giraud (*in* Houard 1911) **n.syn.**

S. consobrinus Giraud (*in* Houard 1911)

S. diaphanus Giraud (*in* Houard 1911)

S. gallaepomiformis (Fonscolombe, 1832)
- *S. longiventris* Giraud (*in* Houard 1911) **n.syn.**

S. subterraneus Giraud (*in* Houard, 1911)
- *S. latifrons* Nieves-Aldrey *et* Martín-Chicote, 1985 **n.syn.**

S. thaumacerus (Dalman, 1823)
- *S. inflatus* Giraud (*in* Houard 1911) **n.syn.**
- *S. vesiculosus* Giraud (*in* Houard 1911) **n.syn.**

S. variabilis Mayr, 1872
- *S. cerridis* Giraud (*in* Houard 1911) **n.syn.**
- *S. conformis* Giraud (*in* Houard 1911) **n.syn.**
- *S. cerricolus* Vassileva-Samnalieva, 1986 **n.syn.**

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